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***Austrocnephia*, new genus, for five species of ‘*Paracnephia*’ (Diptera: Simuliidae), with a key to Australian black fly genera**

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Abstract

A segregate of the so-called Australian ‘*Paracnephia*’ (Diptera: Simuliidae) is assigned to a new genus, *Austrocnephia*. The taxon is fully diagnosed and a key to constituent species presented. Two species-groups are recognized: the *aurantiaca* species-group, comprised of *A. aurantiaca* (Tonnoir 1925) and *A. strenua* (Mackerras & Mackerras 1950), and the *tonnoiri* species-group, comprised of *A. fuscoflava* (Mackerras & Mackerras 1948), *A. orientalis* (Mackerras & Mackerras 1950) and *A. tonnoiri* (Drummond 1931). Both species-groups are diagnosed and the included species fully redescribed. Detailed locality data is given, as is information about biology, when known. Brief comments are offered about the historical biogeography of *Austrocnephia*. A key to Australian simuliid genera is also provided.

Key words: Australia, Diptera, Simuliidae, *Austrocnephia*, *Paracnephia*, black flies, distribution, biology, biogeography, keys

Introduction

The Simuliidae of Australia have long been understudied, the last comprehensive taxonomic treatments of that family having been published during the mid 20th Century (Mackerras & Mackerras *et seq.*, 1948–1955). Indeed, only six additional species were added to the Australian fauna over the ensuing 60 years—the product of isolated species descriptions by Dumbleton (1969), Colbo (1976), Davies & Györkö (1988) and Moulton *et al.* (2004). With just three genera (*Paracnephia*, *Austrosimulium*, and *Simulium s.l.*) and 37 species of black flies recorded from that country (Adler & Crosskey, 2017), it is clear that the Australian fauna is depauperate relative to those of other territories of roughly equal size; for example, Argentina and Chile combined support nine genera and 98 species, whereas the continental United States (excluding Alaska) supports 12 genera and *ca.* 215 species (Adler, 2019).

In an effort to gain a better understanding of Australian black fly diversity, Craig, Moulton & Currie (2017) published the first in a series of five revisions focusing on taxa of Gondwanan provenance. Such species—long referred to as the Australian “*Cnephia*” of authors (and later assigned to the Afrotropical genus *Paracnephia* Rubtsov)—are a heterogeneous assemblage of primitive-grade simuliids now divided among five genera as follows: *Paraustrosimulium* Wygodzinsky & Coscarón 1962; *Bunyipellum* Craig, Currie & Moulton, 2018; *Ectemnoides* Moulton, Currie & Craig 2018; *Nothogreniera* Craig, Currie & Moulton 2018; and *Protaustrosimulium* Currie, Craig & Moulton 2018.

In this paper—the 6th and final contribution in this series—we treat a monophyletic segregate of simuliids characterized, in part, by the distinctive domed yellow-orange thorax of adults. Included are five nominal species previously assigned to *Paracnephia* by Crosskey & Howard (1997); *viz.*, *aurantiaca* Tonnoir 1925; *fuscoflava* Mackerras & Mackerras 1949; *orientalis* Mackerras & Mackerras 1950; *strenua* Mackerras & Mackerras 1950 and *tonnoiri* Drummond 1931. These species are fully re-described and assigned to two species-groups in the new genus *Aus-*

trocnephia, with notes provided about the biogeography of included species. With the conclusion of this series, the Australian simuliid fauna now stands at eight genera and 45 species—a marked increase from the three genera and 38 species known prior to 2017. The first comprehensive key to the revised suite of Australian genera is provided as a springboard for future studies.

Material and methods

A considerable amount of the material examined in this study came from historical collections in Australian museums, in particular the Australian National Insect Collection (ANIC), CSIRO, Canberra. Other notable collections included material taken episodically by P. and H. Zwick from the early 1970's through the early 2000's, plus material collected by JKM in 1996. The latter was fixed in 95% ETOH and stored at minus 20°C, preserving the material in pristine condition. Extensive additional collections of fresh material were made by JKM, DCC and DAC in 2014 and 2015. Other sources of material are indicated later.

When possible, a paratype specimen was dissected and slide mounted, or the parts placed in a microvial back on the pin. Types held at the ANIC were examined by LHG-A in 2007. Dissection techniques and photography were as described by Gil-Azevedo & Maia-Herzog (2007) and Craig *et al.* (2012). Unless indicated, all images here are by DAC and follow Craig *et al.* (*loc. cit.*: 50). Images by LHG-A were taken using a Leica macroscope with a proprietary stacking program. All images here have been manipulated—namely background removal and replacement, using Photoshop™ CS6. We fully illustrate structures of *A. aurantiaca*, but typically illustrate only diagnostic structures of the other species. For particularly variable species such as *A. aurantiaca*, we provide extra images to illustrate the range of variation in particular structures.

Terms for structures follow mainly those of Adler *et al.* (2004), with some exceptions, such as use of 'basal tooth' as opposed to 'thumblike lobe' for the secondary denticulation on bifid tarsal claws of females. Further, we retain the convention of considering the basitarsus as tarsomere I; hence, the calcipala is situated on the inner apical margin of tarsomere I, and the pedisulcus, if present, is situated at the dorsal base of tarsomere II. We also use the term 'paramere connector' (p c) (*e.g.*, Figs. 78, 147, 179) —a posteriorly directed strap-like structure that connects the basal arm of the ventral plate to the paramere. Primitively in simuliids, the connector is markedly elongate and originates near the anterior apex of the basal arm, as exemplified by members of the Parasimuliinae Smart and Prosimuliini (Wood & Borkent, 1982; Adler *et al.*, 2004). Among simuliines, the paramere connector originates much more basally on the arms, with a trend towards reduced expression. In *Austrocnephia* and other members of the Australian Gondwanan simuliids, the paramere connector, although originating more basally on the basal arms, retains a distinct strap-like appearance, unlike most other simuliines where the parameres are connected by an angular process on the side of the ventral plate. We consider the condition in *Austrocnephia* to represent an intermediate stage of a transformation series between the primitive and derived states.

For wings we give the 'a:b ratio' (*e.g.*, Fig. 9), where 'a' is the length of the basal radial cell (br) from the wing base to the r-m vein junction, and 'b' is the length from r-m to the wing apex (McAlpine, 1981). We follow Cumming & Wood (2017) and de Moor (2017) regarding homologies of wing veins (Figs. 8, 9).

For pupae, we provide the following ratios of the frons for both males and females: basal width to maximum width towards the vertex and basal width to maximum length. For larvae, rather than using the nomenclatural system for hypostomal teeth developed by Currie (1986) and adopted by Adler *et al.* (2004), we use a numbering scheme suggested by JKM (similar to that proposed by Okazawa & Nodasaka, 1982) and used by Craig *et al.* (2018a, b), Currie *et al.* (2018) and Moulton *et al.* (2018). The 'median tooth' is assigned a '0', and those lateral on either side are numbered in sequence '1, 2, 3'. Thus, the 'lateral or corner tooth' is '4' and the so-called 'paralateral teeth' are designated 5–8 (*i.e.*, a total of 17 teeth appears here to be the ground plan) (*e.g.*, Figs. 44, 189).

Distinctive of certain larvae of *Austrocnephia*, and in particular *A. strenua*, are lateral structures that extend from the base of the distal article of the prothoracic proleg (Fig. 95). Mackerras & Mackerras (1950: 170, 186) referred to these structures as 'palp-like processes', whereas Colbo (1974: 69) called them 'lapets' (*sic*). We here refer to them as 'lappets' (*i.e.*, defined as small lobe-shaped organs—Century Dictionary & Cyclopedia, and others). Larvae of some species in the genus have additional arms on the anal sclerite other than the typical posteroventral arms—such are referred to as 'posterolateral arms' (*e.g.*, Figs. 54, 96).

Many older localities (as cited in the literature from the early to mid 1900's) are no longer identifiable with certainty. Even in instances where historical collection sites can reasonably be inferred, the hydrology of the wa-

tercourse is often modified due to the construction of weirs and other landscape modifications (*e.g.*, Moulton *et al.*, 2018: 10). We have, nonetheless, attempted to provide GPS coordinates for all localities—even if only to identify the general region where a historical collection was taken. GPS data, with an error of *ca.* 30 m, is given for all material collected by us. Localities, are grouped by State and, where possible, listed from north to south (Figs. 196, 197).

We have also attempted to provide locality data in a standard format, giving State, region, locality name, GPS, date, stage, collector and a coden (see later) for institutes where material is deposited. Localities derived from literature are given with the appropriate citation. Material from the Tasmanian Museum and Art Gallery (TMAG), Rosny, Hobart, was accumulated during an Australian River Assessment System (AusRivAS), undertaken by the State's Department of Primary Industries, Parks, Water and Environment (DPIPWE), the aim of which was to allow prediction of the invertebrate community composition of a river. These collections have their own unique locality code, *e.g.*, GFOR17. Locality listings are far from exhaustive—for example, the Victoria AusRivAS collections and those of other States were not examined.

Given the great variety of material available for study and range of habitats, and wide distribution of certain species, we provide locality information in the caption for images. Furthermore, since the Mackerras' papers (1948, *et seq.*) are incremental, for convenience here, we provide a page number for most citations, and follow this, in large part, for others.

Label data, when reported, uses square brackets [] to indicate a label and a slash / for separate lines of text. Male and female signs are indicated as {M} and {F}.

Codens for institutions known to hold Austrocnephia material

AM	Australian Museum, Sydney, NSW, Australia.
ANIC	Australian National Insect Collection, CSIRO, Canberra, ACT, Australia.
JKM	Private collection of JKM, currently University of Tennessee, Knoxville, TN, USA.
MM	Melbourne Museum, Carlton, Melbourne, Victoria, Australia.
TMAG	Tasmania Museum and Art Gallery, Rosny, Hobart, Tasmania, Australia.
QM	Queensland Museum, Brisbane, Australia.
ROM	Royal Ontario Museum, Toronto, Ontario, Canada.
UASM	Strickland Museum, Biological Sciences, University of Alberta. Edmonton, Canada.
WMH	West Mead Hospital, Sydney Medical School, University of Sydney, Australia

***Austrocnephia* n. gen. Craig, Currie, Gil-Azevedo & Moulton**

Type Species: *Simulium aurantiaca* Tonnoir 1925: 234

Diagnosis. *Adults*: moderate to large-sized species (total body length 2.2–5.0 mm) with yellow-orange thorax, both sexes with markedly domed thorax. Antenna with nine flagellomeres. *Female*: frons narrowed; sensory vesicle of palpomere III half or more length of article, (terminal) palpomere V elongate; mandible with teeth only on medial side except *strenua*; cibarium unarmed, cornuae flared posteromedially and well sclerotized apically; wing a:b ratio 1.0:2.5–2.7, basal medial cell poorly expressed or absent, apex of wing and anal lobe slightly fumose, anterior veins yellowish, as is membrane, pigmentation at junction of r-m cross vein and R_1 absent to strongly expressed, costa with both hair-like and spine-like setae, the latter of varied thickness and color; apices of R_1 and R_s not joined together or closely appressed before joining C, R_s slightly branched apically in *aurantiaca* species-group, unbranched in *tonnoiri* species-group, CuA slightly sinuous, CuP extended essentially to wing margin, as also A_1 in some species; katapisternum as wide as deep, sulcus wide and shallow; metathoracic furcasternum with flange on dorsal arms; hind basitarsus with distinct row of ventral spines and calcipala well-developed, tarsomere II with poorly expressed pedisulcus usually obscured by calcipala; claw bifid, with basal tooth moderately-to-well expressed, directed slightly laterally, claw heel scarcely-to-moderately expressed; cercus and anal lobe elongated; spermatheca darkly pigmented, surface smooth to somewhat wrinkled, with variously-sized membranous area at junction with spermathecal duct. *Male*: eye with relatively few (15–20) large upper ommatidia; gonocoxa strengthened postero-medially and fluted, gonostylus quadratic to cone-shaped, typically with two or three (rarely four) apical spines;

ventral plate with apex directed slightly- to markedly ventrally, basal arms moderately elongate, paramere connector short but substantial; median sclerite not markedly developed; parameres plate-like, triangular, size various; parameral spines absent, although variously expressed substantial microtrichia may be present on adjacent aedeagal membrane; dorsal sclerite absent. *Pupa*: gill arborescent, consisting of 21–50 short, pseudoannulated filaments; head without postorbital spine on ocular sclerite; head and thorax not tuberculate; dorsocentral setae with curled tips; abdomen with tuberculae poorly expressed or absent, but well expressed in *tonnoiri*, posterior abdominal segments with pleurites present in *tonnoiri* species-group, absent in *aurantiaca* species-group, grapnel-like hooks absent from segment IX. *Cocoon*: silk of irregular weave, cocoon poorly defined, covering abdomen and thorax of pupa, and incorporating various amounts of foreign material. *Larva*: body relatively robust; first instar larvae with well-developed labral fans; antenna with distal article subequal in length to medial article, not extended beyond labral fan stem; cephalic sensilla not markedly expressed; first mandibular spinous tooth of normal length to markedly elongated; cervical sclerites typically connected to postocciput by narrow strap; hypostoma with teeth either borne on three variously expressed lobes, or teeth arranged in delta-like fashion with tooth 0 most prominent; post-genal cleft small, inverted-U or subrectangular shaped, extended less than quarter distance to hypostomal groove; posterior tentorial pits either rectangular or rounded in shape; prothoracic proleg lappets present, or absent; lateral plate of proleg either L- or V-shaped; abdominal segment nine without ventral tubercles; rectal papillae of three simple lobes; anal sclerite with posteroventral arms markedly developed, in some species with posterolateral arm also; membrane between arm and circlet of hooks with either many or few campaniform sensilla; posteromedial gap between ventral arms either open or closed (hole); posterior circlet of hooks markedly expressed and directed slightly ventrally, some species with large numbers of hooks.

Etymology. The name *Austrocnephia* preserves the original assignment of these species to *Cnephia* (an otherwise exclusively northern hemisphere taxon), while reflecting the geographical endemism of the segregate. The gender is feminine.

Distribution. The genus is widely distributed in mesic subtropical and temperate areas along the eastern and southern seaboard of Australia. Most species range from the Atherton Tablelands near Cairns, Queensland, south along the Great Divide Mountains to Victoria and Tasmania, then westward to southeastern-most South Australia. One species, *Austrocnephia tonnoiri*, however, is disjunct from the others in the southwestern-most corner of Western Australia and there occurs sporadically in fast flowing portions of more productive, often lower gradient streams. *Austrocnephia fuscoflava* of the *tonnoiri* species-group appears to be restricted to lowland coastal streams of southeastern Queensland. *Austrocnephia orientalis* is also sporadic in distribution. Detailed locality data is given for each species, as is a distribution map for each species-group (Figs. 196, 197).

Remarks. Monophyly of the five species considered herein is supported by a suite of diagnostic character states, *inter alia*: adult thorax yellow/orange and markedly domed; wing vein CuA only slightly curved; maxillary palp of female with sensory vesicle *ca.* two-thirds length of palpomere III; cercus of female distinctly longer than length of anal lobe; larva with abdomen elongate, expanded at segments VII and VIII, tapered markedly to posterior proleg on segment IX. While none of these character-states by themselves is unique within the Simuliidae, taken collectively, they are constitutive for the five species at this phylogenetic level. *Austrocnephia aurantiaca* and *A. tonnoiri* are morphologically variable, probably representing complexes. Cytological and/or molecular analyses are needed to clarify the specific boundaries of nominal species recognized in this study. Two species groups are recognized to reflect the overall similarity of included species.

Constituent species. The following described species are assigned to *Austrocnephia* **n. gen.** and new combinations therefore established.

aurantiaca species-group: *Austrocnephia aurantiaca* (Tonnoir 1925) **n. comb.**, *A. strenua* (Mackerras & Mackerras 1950) **n. comb.**

tonnoiri species-group: *Austrocnephia fuscoflava* (Mackerras & Mackerras 1949) **n. comb.**, *A. orientalis* (Mackerras & Mackerras 1950) **n. comb.**, *A. tonnoiri* (Drummond 1931) **n. comb.**

Key to the species of *Austrocnephia*

Adults

1. Junction of r-m cross vein and R₁ with spot at most faintly expressed (Figs. 9, 18, 59, 64); male ventral plate with apex markedly narrowed (Figs. 27, 78) *aurantiaca* species-group ... 2

- Junction of r-m cross vein and R_1 with markedly expressed dark spot (Figs. 105, 165, 176); male ventral plate apex not markedly narrowed (Figs. 119, 147, 179). *tonnoiri*-species-group ... 3
- 2. Thorax overall yellow-orange; calcipala about as long as wide (Fig. 10); palpomere V of female 2–3× longer than palpomere IV (Fig. 5); sensory vesicle of palpomere III *ca.* 2/3 length of article (Fig. 5); genital fork anterior stem subequal in length to lateral arms (Fig. 15); spermatheca surface markedly wrinkled (Fig. 16); male gonostylus narrow in ventral view, broad in lateral view, markedly curved posterodorsally, with three apical spines (Fig. 26). *A. aurantiaca*
- Thorax overall dark orange; calcipala markedly longer than wide (Fig. 65); palpomere V of female equal in length or shorter than palpomere IV, sensory vesicle of palpomere III *ca.* 1/2 length of article; spermatheca not markedly wrinkled (Fig. 70); male gonostylus narrow in ventral view, broad in lateral view, more angulate posterodorsally, with two apical spines (Fig. 77) *A. strenua*
- 3. Western Australia (Fig. 197). Female: frons broad, at narrowest point broader than antennal base; clypeus and labrum well developed (Fig. 166); mandible with *ca.* 28 teeth medially; claw with basal tooth less than 1/3 length of main talon (Fig. 168) *A. tonnoiri*
- Eastern Australia (Fig. 197). Female: frons narrower, at narrowest point about as broad as antennal base; clypeus and labrum less-well developed (Figs. 101, 134); mandible with *ca.* 22 small teeth medially (Figs. 103, 135); claw with basal tooth 1/2 length of main talon (Fig. 108). 4
- 4. Female: frons narrowed ventrally (Fig. 101); genital fork anterior stem not markedly bowed ventrally near junction with lateral arms (Fig. 111). Male: head depth as long as scutum in lateral view (Fig. 114) *A. fuscoflava*
- Female: frons more parallel-sided; genital fork with anterior stem bowed ventrally near junction with lateral arms (Fig. 140). Male: head depth shorter than scutum length in lateral view (Fig. 143) *A. orientalis*

Pupa

- 1. Abdominal segments V–VII without conspicuous pleurites, represented at most by small sclerotized area at base of pleural spines; sternite V with 5+5 or 6+6 hooks (Figs. 35, 87) *aurantiaca* species-group ... 2
- Abdomen: segments V–VII each with a distinct pleurite; sternite V with 3+3 hooks (Figs. 124, 153, 184). *tonnoiri*-species-group ... 3
- 2. Gill with 30–40 filaments arising from short, stout, primary trunks (Fig. 32); abdominal sternite V with 6+6 hooks (Fig. 35) *A. aurantiaca*
- Gill with 42–56 filaments arising from longer, more slender, primary trunks (Figs. 81, 84); abdominal sternite V with 5+5 hooks (Fig. 87) *A. strenua*
- 3. Gill with 45–75 slender filaments arising from short primary trunks (Figs. 148, 151). Widely distributed in eastern Australia (Fig. 197) *A. orientalis*
- Gill with 15–40 thicker filaments arising from more elongate primary trunks (Figs. 123, 182). Southeastern-most Queensland or southwestern-most Western Australia (Fig. 197). 4
- 4. Southeastern Queensland (Fig. 197). Head and thorax slightly rugose, bearing scattered tubercles; gill with 15–20 filaments (Fig. 123) *A. fuscoflava*
- Western Australia (Fig. 197). Head and thorax smooth, without tubercles; gill with 20–40 filaments (Fig. 182) . . . *A. tonnoiri*

Larva

- 1. Antenna with distal article shorter than medial article (Fig. 39); hypostoma without lateral serrations (Fig. 45); anal sclerite with posteroventral arms markedly thickened and darkly sclerotized, with large numbers of adjacent campaniform sensilla (Figs. 52, 53) *aurantiaca* species-group ... 2
- Antenna with distal article longer than medial article; hypostoma with lateral serrations (Fig. 129); anal sclerite with posteroventral arms not markedly thickened or darkly sclerotized, with relatively fewer adjacent campaniform sensilla (Fig. 131) *tonnoiri* species-group ... 3
- 2. Hypostoma with apex of tooth 0 extended anteriorly to about the same level as that of tooth 4, giving anterior margin of hypostoma a trilobed appearance; prothoracic proleg lappets either absent or weakly expressed, shorter than apical article of proleg (Fig. 50, 51); anal sclerite without posterolateral arm (Figs 52, 53), rarely with it slightly developed (Fig. 54) *A. aurantiaca*
- Hypostoma with apex of tooth 0 extended anteriorly markedly beyond that of tooth 4, giving anterior margin of hypostoma a delta-like appearance; prothoracic proleg with lappets well developed, about the same length as apical article of proleg (Fig. 95); anal sclerite with well-developed posterolateral arm (Fig. 96). *A. strenua*
- 3. Western Australia. Posterior proleg with 120 rows of *ca.* 24 hooks per row (Fig. 192) *A. tonnoiri*
- Eastern Australia. Posterior proleg with 115 or fewer rows of *ca.* 20 or fewer hooks per row (Fig. 131) 4
- 4. Abdominal segments 7 & 8 markedly expanded ventrally (Fig. 125). Southeastern-most corner of Queensland (Fig. 197) *A. fuscoflava*
- Abdominal segments 7 & 8 not markedly expanded ventrally (Fig. 154). Widely distributed in eastern Australia (Fig. 197) *A. orientalis*

aurantiaca species-group

Diagnosis. *Adults:* larger, lighter-colored species, female total body length 2.8–5.5 mm; vein R_s slightly thickened

distally, or with evidence of branching; junction of r-m cross vein and R_1 with faintly expressed dark spot or, if spot not evident, then with r-m cross vein darker than adjacent veins; pedisulcus absent, represented at most by a slight wrinkling of cuticle on dorsal base of hind tarsomere II; tarsal claw basal tooth a third or less length of main talon, claw heel moderately expressed; genital fork with anterior stem of normal width, not markedly bent; male gonostylus angulate, with two or three apical spines; ventral plate with apex markedly narrowed in ventral view, apex directed ventrally, producing concave appearance; parameres well sclerotized and distinct. *Pupa*: gill with numerous (38–50) filaments; abdominal tuberculation absent; pleurites absent from segments VI & VII. *Larva*: mandible apex with spinous teeth markedly expressed; hypostomal teeth 5–7, poorly expressed; lateral hypostomal serrations absent; posterior tentorial pits rectangular; prothoracic proleg lateral sclerite L-shaped, lappets not commonly present; anal sclerite with posterolateral arms variously present; area between posterolateral arms and circlet of hooks with large number of campaniform sensilla; posterior proleg with large number (10,000–17,000) of hooks; larvae occur in flows of high velocity.

***Austrocnephia aurantiaca* (Tonnoir 1925). New combination.**

(Figs. 1–57)

Simulium aurantiacum Tonnoir 1925: 234; original designation.

Simulium (*Cnephia*) *aurantiacum*. Edwards, 1931: 147.

Cnephia aurantiacum. Smart, 1945: 498. Mackerras & Mackerras, 1948: 238. 1949: 383.

Cnephia A. Rothfels, 1979: 522; cytological study, perhaps *aurantiacum*?

‘*Cnephia* of authors’ *aurantiacum*. Crosskey, 1987: 443; undetermined genus, Prosimuliini.

aurantiacum. Crosskey, 1989: 222; unplaced species of Prosimuliini.

Paracnephia aurantiaca. Crosskey & Howard, 1997: 18; new combination.

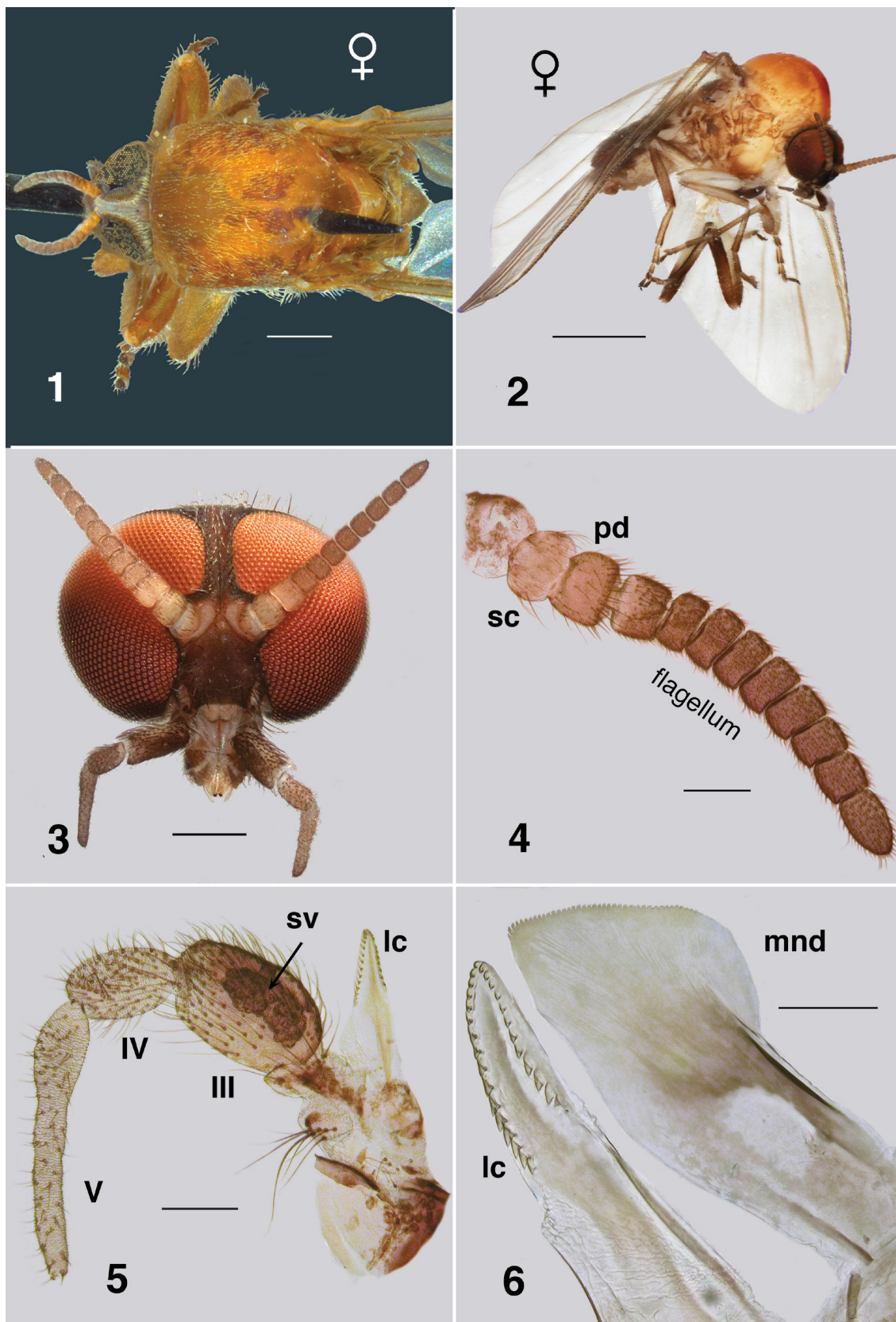
Paracnephia aurantiaca. Bugledich, 1999: 327.

‘*Cnephia*’ *aurantiacum*. Moulton, 2000: 98. Moulton, 2003: 47.

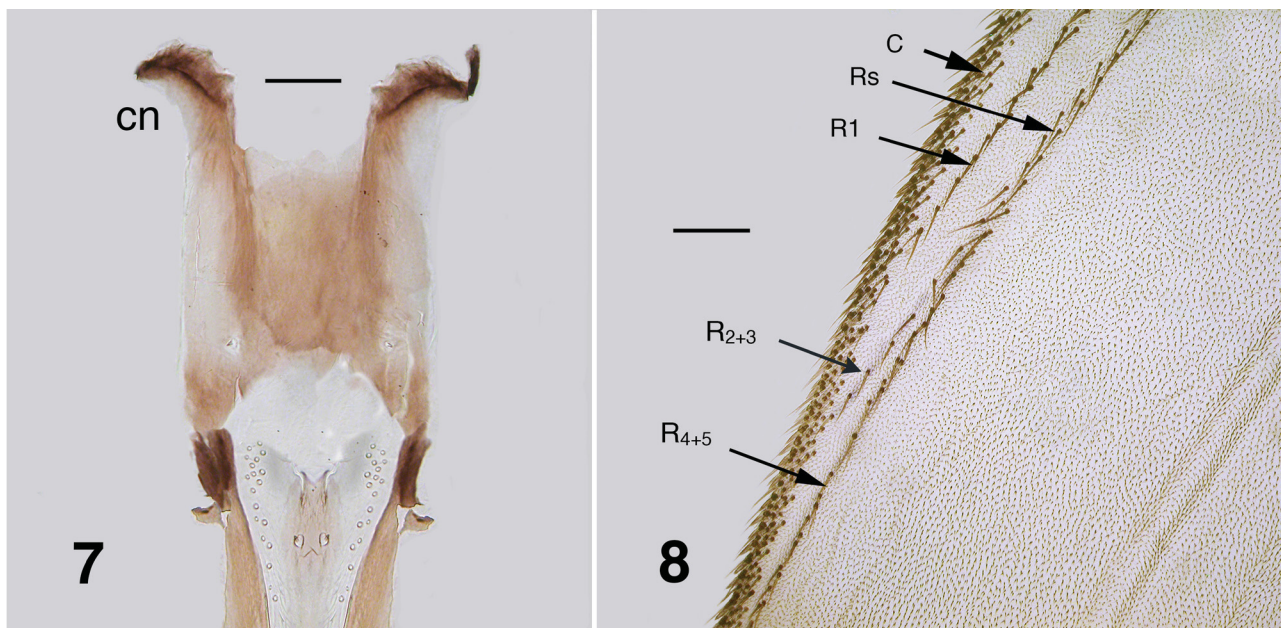
Paracnephia aurantiaca. Crosskey & Howard, 2004: 10; unplaced to subgenus.

Paracnephia aurantiaca. Adler & Crosskey, 2008: 28; transferred to Simuliini, unplaced to subgenus. Hernández-Triana *et al.* 2017: 350. Adler, 2019: 32.

Redescription. *Adult female* (based on three paratypes and numerous other specimen). *Body* (Figs. 1, 2): head dark orange, thorax yellowish orange, abdomen blackish; total length 3.2–5.0 mm. *Head* (Fig. 3): overall dark in colour; width 0.96 mm; depth 0.70 mm; postocciput densely hirsute with long pale hairs, frons parallel-sided, not markedly narrow, dark brown-black, sparse long black hairs laterally; frons:head-width ratio 1.0:12.0. *Eye*: interocular distance *ca.* 0.1 mm; upper ommatidia reddish orange, lower ommatidia darker, ommatidia diameter 0.022 mm; *ca.* 36 rows across and 44 down at mid-eye. *Clypeus*: width 0.29 mm; mottled dark brown, vestiture of long hairs laterally. *Antenna* (Figs. 3, 4): elongate, extended well beyond posterior margin of head; total length 0.95 mm; scape and pedicel pale, similar in size to flagellomere I; flagellomere II–VII similar in size and shape, flagellomeres VIII & IX slightly more elongated. *Mouthparts*: feebly developed, *ca.* 0.28× length of head depth; maxillary palp (Fig. 5) total length 0.83 mm, palpomeres I & II small, palpomere III broader and darker than other palpomeres, proportional lengths of palpomeres III–V 1.0:0.8:1.6, respectively; sensory organ moderately elongated, 0.33–0.50× length of palpomere III, opening small, 0.2× vesicle width; mandible (Fig. 6) with *ca.* 30 weakly developed inner teeth, outer teeth absent; lacinia with 16 and 10 teeth on inner and outer edge respectively; cibarium (Fig. 7) with cornuae sclerotized apically and lightly sculpted, medial gap angulate. *Thorax*: length 1.2–1.8 mm; width 1.2–1.3 mm; evenly yellowish orange; postpronotal lobe well developed with longer hair than on scutum; scutellar depression with similar vestiture; scutellum slightly paler than scutum, vestiture of sparse very fine yellowish hairs; postnotum concolourous with scutellum, vestiture similar; anteppronotal lobe with dense patch of yellow hairs; proepisternum and fore coxa with sparse hairs; anepisternal (aka plural) membrane yellowish brown, bare; katepisternal dark brown, sulcus shallow and broad. *Wing* (Figs. 8, 9): length 4.1–5.0 mm; width 1.6–2.2 mm; membrane slightly fumose on apex and anal lobe; veins dark orange; costa with mixture of thin and thickened hairs on distal 2/3rds, the latter not markedly darkened; R_s narrowly divided distally (R_{2+3} occasionally expressed as row of a few fine hairs); a:b ratio 1.0:2.5; r-m cross vein darker than adjacent veins, but pigmentation not extended into surrounding membrane; basal medial cell minute or absent; M_1 appearing doubled or tripled; CuA not markedly sinuous; CuP extended nearly to wing margin, as does A_1 . *Haltere*: stem clear, knob yellowish orange. *Legs* (Fig. 10): forelegs evenly pale; mid and



FIGURES 1–6. *Austrocnechia aurantiaca* female. (1) Dorsal view of paratype. (Mount Wilson). Image by LHG-A. Scale bar = 0.5 mm. (2) Habitus. (Steavenson Falls). Scale bar = 1.0 mm. (3) Frontal view of head. (Steavenson Falls). Scale bar = 0.2 mm. (4) Antenna, showing flagellum, pedisulcus (pd) and scape (sc). (Brindabella). Scale bar = 0.1 mm. (5) Maxillary palp, showing palpomeres III–V, sensory vesicle (s v) and lacinia (lc) (Brindabella). Scale bar = 0.1 mm. (6) Mandible (mnd) and lacinia (lc). (Steavenson Falls). Scale bar = 0.05 mm.



FIGURES 7, 8. *Austrocnephia aurantiaca* female. (7) Cibarium showing cornuae (cn). (Steavenson Falls). Scale bar = 0.05 mm. (8) Wing veins showing branched Rs. (Brindabella). Scale bar = 0.1 mm.

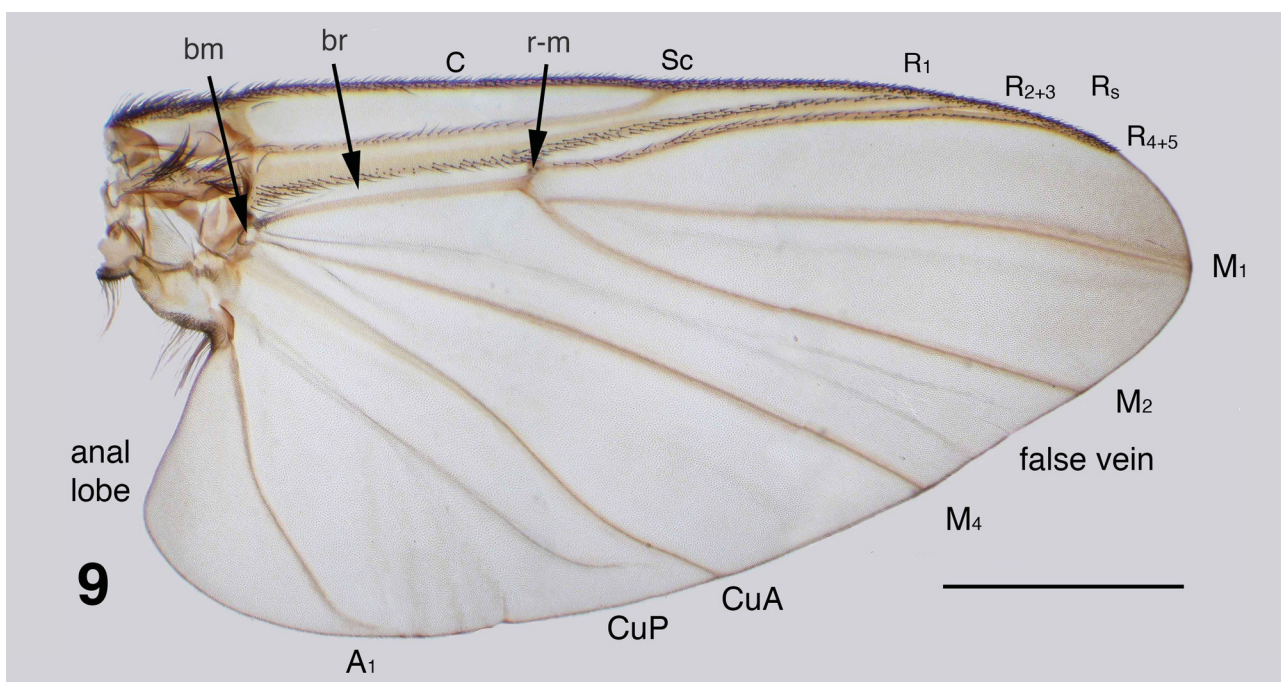
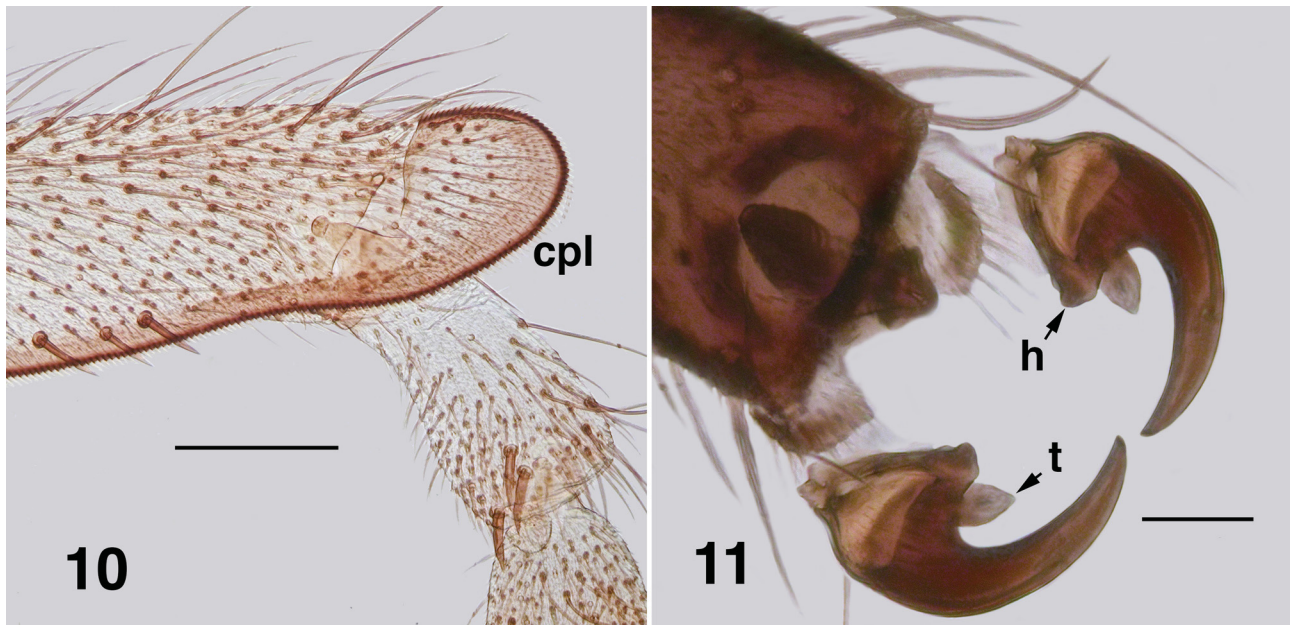


FIGURE 9. *Austrocnephia aurantiaca* female. (9) Wing, showing veins and basal medial cell (bm) and basal radial cell (br). (Brindabella). Scale bar = 1.0 mm.

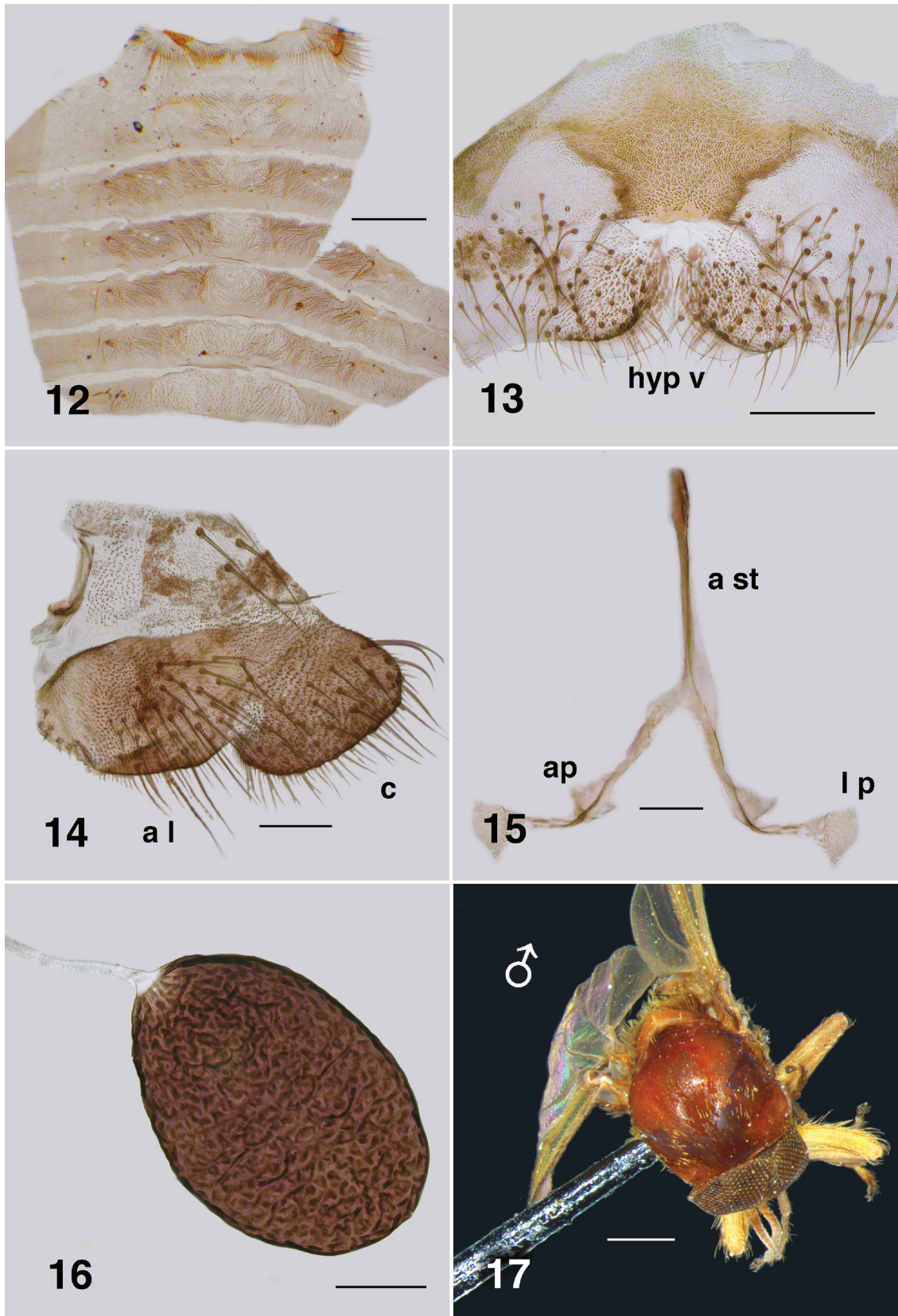
hind legs medium brown; hind basitarsus with ventral row of regular stout spines; calcipala subequal in length and breadth; pedisulcus absent; tarsomere II 2.0–2.4× as long as distal width; claw (Fig. 11) with main talon strongly curved and evenly tapered, basal tooth 0.25–0.50× length of talon, heel substantial and angulate. *Abdomen* (Fig. 12): basal scale (tergite I) dark brown, vestiture of long dense hairs; anterior few segments pale and yellowish, other segments mottled dark brown; tergites lightly sclerotized, barely discernable from remainder of dorsum, broader in posterior segments; vestiture better expressed on posterior segments. *Genitalia*: markedly small; sternite VIII with distinct microtrichial array medially, with larger stronger hairs posterolaterally; hypogynial valves (Fig. 13), lightly pigmented, vestiture of triads of microtrichia and strong hairs, medial edges of valves slightly concave, but not touching, broadly rounded apically, valves slightly domed medially; cercus in lateral view (Fig. 14) elongated

with slight medial depression, anal lobe also elongate, both with vestiture of long hairs; genital fork (Fig. 15) with anterior stem relatively long and narrowed, slightly expanded apically, no indication of membranous lateral areas, lateral arms narrow, apodeme as membranous triangular region, lateral plates small, trapezoidal- or subtriangular-shaped; spermatheca ovoid (Fig. 16), markedly wrinkled, without internal spines, membranous area at junction with spermathecal duct small.

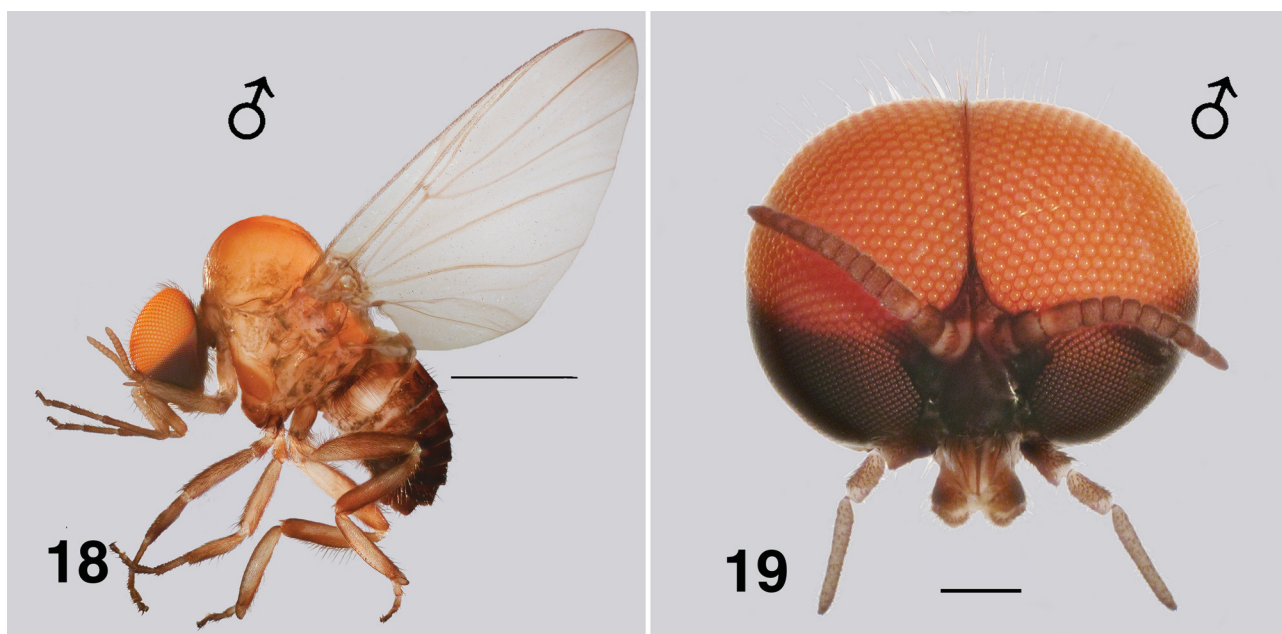


FIGURES 10, 11. *Austrocnephia aurantiaca* female. (10) Calcipala (cpl) and tarsomere II. (Steavenson Falls). Scale bar = 0.1 mm. (11) Tarsal claws, heel (h) and basal tooth (t). (Brindabella). Scale bar = 0.02 mm.

Adult male (based on a paratype and numerous other specimens). *Body*: overall yellow including head and thorax, abdomen black (Figs. 17, 18); total body length variable, specimens from Pretty Valley, VIC. 3.3–4.5 mm; those originally described by Tonnoir (1925: 234) 2.0–2.5 mm. *Head* (Fig. 19): width 0.98 mm; depth 0.7 mm. *Eyes*: upper ommatidia dark orange, not markedly enlarged, diameter 0.04 mm, *ca.* 23 across and down; lower ommatidia black to blackish orange, markedly smaller, diameter 0.02 mm, *ca.* 24 across, 38 down. *Clypeus*: black; width 0.19 mm; vestiture of sparse fine black hairs. *Antenna* (Fig. 20): total length 0.71–0.75 mm; pedicel and scape dark brown; scape short, pedicel wider than broad, flagellomere I narrower than scape and longer than broad, pale basally, other flagellomeres evenly medium brown and tapered slightly to apical flagellomere. *Mouthparts*: insubstantial; length $0.3\times$ head depth; maxillary palp (Fig. 21) 0.68 mm long, palpomeres I & II small, palpomeres III & IV subequal in length, palpomere V fine and elongated, proportional lengths of palpomeres III–V 1.0:0.8:1.7 respectively, sensory vesicle small, spherical, occupying $0.22\times$ or less palpomere length, opening $0.33\times$ vesicle width; lacinia small, lacking teeth, but with apical hairs; mandible lacking teeth. *Thorax*: length 1.4 mm; width 1.3 mm; markedly domed, lateral outline semicircular, head angled anteriorly; postpronotal lobe concolourous with scutum, bearing long fine pale hairs; antepronotal lobe with patch of sparse fine pale hairs; proepisternum bare; scutum evenly pale yellow, vestiture of sparse long fine pale hairs, longer in scutellar depression; scutellum lighter than scutum, with markedly long yellow hairs laterally; pleurae yellow, anepisternal membrane bare; katapisternum brown, sulcus distinct, but shallow. *Wing*: length 3.7–4.3 mm, width 1.7–2.3 mm; membrane slightly fumose at apex, anal lobe very slightly so; anterior veins dark orange; costa with mixture of thin and thickened hairs; Rs narrowly but distinctly branched distally (Fig. 22); a:b ratio 1.0:2.6; basal medial cell present, but minute; M_1 appearing doubled or tripled, CuA not markedly sinuous; CuP extended nearly to wing margin. *Haltere*: stem pale, knob tan. *Legs*: overall yellowish, hind leg with darker coloured distal tibia; hind basitarsus, slightly expanded medially with ventral row of stout spines, calcipala and pedisulcus as for female; tarsomere II $2.6\times$ as long as distal width; tarsal claw with short talon, grappling hook of 25–27 teeth (Fig. 23). *Abdomen* (Fig. 24): black dorsally and posteriorly, pale anteroventrally, vestiture of markedly long golden hairs, more so anteriorly; basal scale (tergite I) black, hairs markedly golden and long, extended to posterior of tergite II; tergite II V-shaped, remainder broad; sternite I present, sternite II absent, sternites III–VIII rounded, distinctly hirsute. *Genitalia* (Fig. 25): small and lightly sclerotized; cerci well developed;



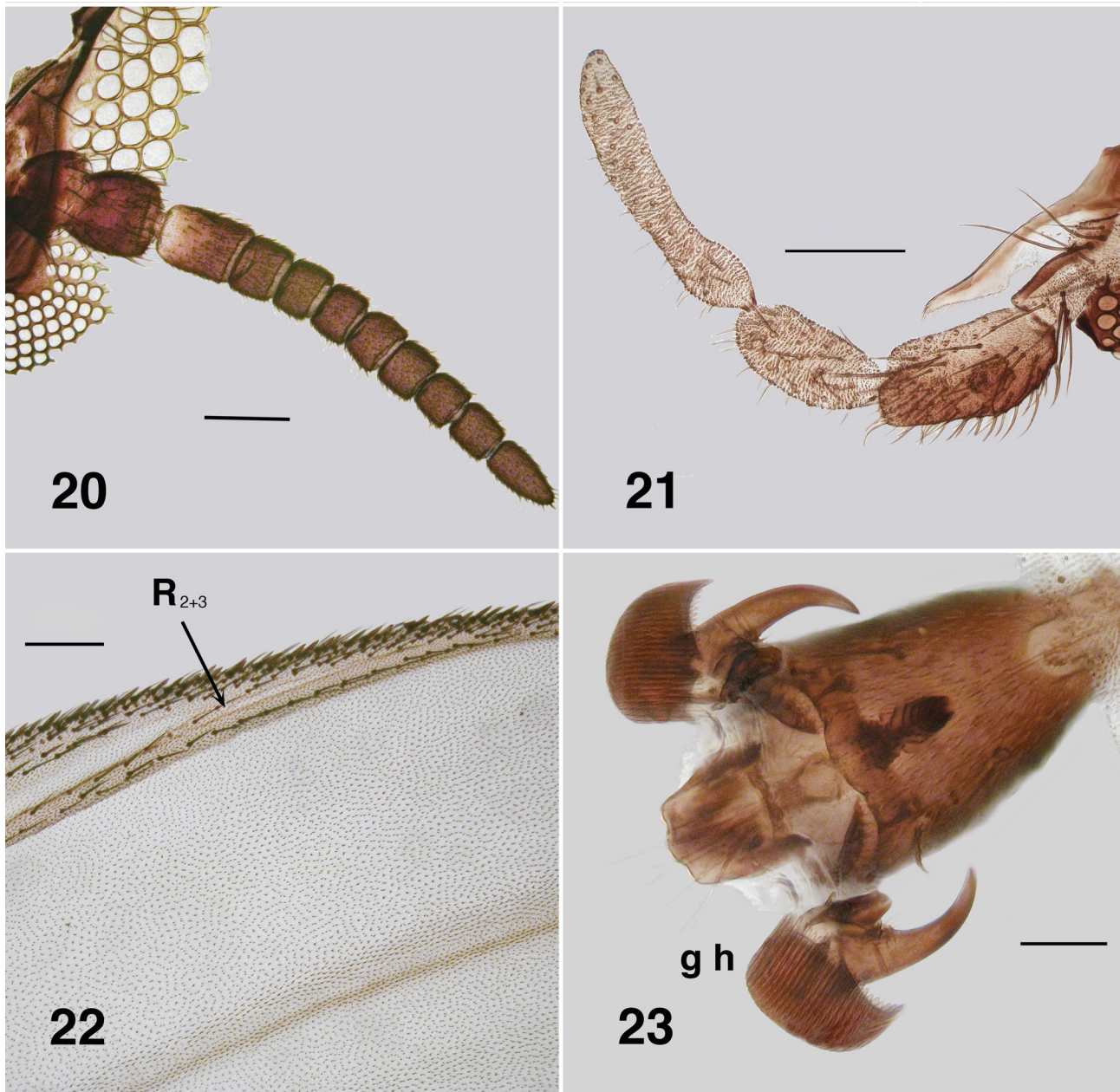
FIGURES 12–16. *Austrocnephia aurantiaca* female. (12) Abdominal tergites. (Brindabella). Scale bar = 1.0 mm. (13) Hypopygial valves (hyp v). (Brindabella). Scale bar = 0.1 mm. (14) Anal lobe (a l) and cercus (c). (Brindabella). Scale bar = 0.05 mm. (15) Genital fork, anterior stem (a st), apodeme (ap) and lateral plate (l p). (Brindabella). Scale bar = 0.05 mm. (16) Spermatheca. (Steavenson Falls). Scale bar = 0.1 mm. **FIGURE 17.** *Austrocnephia aurantiaca* male. (17) Holotype. (Mount Wilson). Image by LHG-A. Scale bar = 1.0 mm.



FIGURES 18, 19. *Austrocnephia aurantiaca* male. (18) Habitus. (Taggerty River). Scale bar = 1.0 mm. (19) Frontal view of head. (Brindabella). Scale bar = 0.2 mm.

gonocoxa $1.1\times$ longer than its basal width, vestiture of long black sparse hairs and microtrichia; gonostylus $1.6\times$ longer than basal width, markedly shorter than gonocoxite, narrow in ventral view, broad in lateral view (Fig. 26), with two or three apical spines; ventral plate small, $1.6\times$ wider than long in ventral view, apex directed ventrally producing appearance of medial concavity, vestiture absent except for a few hairs medially (Fig. 27), basal arms elongated and narrow; median sclerite in the form of two short, darkly sclerotized, arms arising from anterior edge of ventral plate; parameres plate-like basally, tapered distally; adeagal membrane with 7–15 short stout spines near apex of paramere, membrane otherwise adorned with microtrichia.

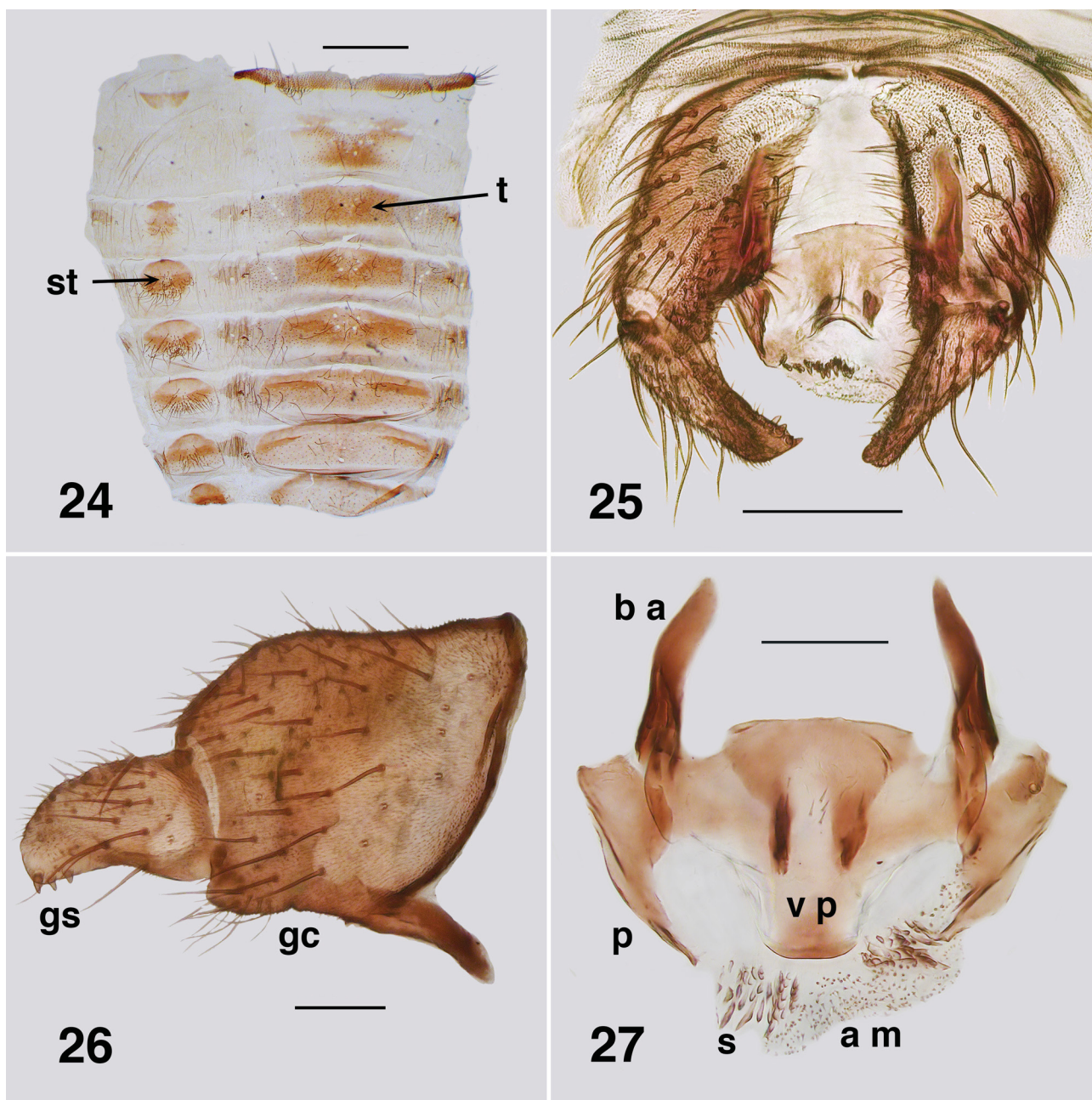
Pupa (based on numerous specimens). *Body*: female length 3.3–4.0 mm, male length 3.3–3.8 mm (Fig. 28). *Head*: frons of female truncated with ratio of basal width to vertex width 1.0:1.5, and basal width to length 1.0:1.7 (Fig. 29), that of male more ovoid (Fig. 30), ratios 1.0:1.9 and 1.0:3.1 respectively; cuticle faintly patterned; frontal and facial setae present, epicranial setae present near antennal sheath; postorbital spine absent; antennal sheath of female with apex extended beyond margin of ocular shield, that of male not extended to margin of ocular shield. *Thorax*: markedly domed, smooth, with dorsal setae trichoid, short, curved, but not curled at tip (Fig. 31). *Gill*: total length *ca.* 1.3–1.5 mm, with 40–50 light brown filaments arising from 5 or 6 short trunks (Fig. 32); filaments paler apically, some branched at irregular distances from base; ventral filaments directed anteriorly, dorsal filaments directed mainly dorsally, but with one or two longer filaments reflexed posteriorly over thorax; filament surface pseudoannulated throughout (Fig. 33). *Abdomen* (Fig. 35): well sclerotized, especially the anterior tergites, with minute rounded tubercles; tergites III & IV extended more ventrad than other tergites, separated from pleurite by narrow band of striate membrane; tergite V separated from pleurite by band of striate membrane; pleurites absent from segments V & VI; sternites VI & VII divided medially by a semimembranous longitudinal band, sternite VIII a single lightly sclerotised plate with medial marking. Abdominal armature moderately well developed; tergite I with fine hairs; tergites II–IV each with 4+4 dorsal and 3+3 lateral anteriorly directed recurved hooks, the latter smaller than dorsal hooks; tergite V with four hairs and poorly expressed spine comb; tergites VI & VII each with a well-developed transverse row of spine comb, plus a double pair of fine hairs anteriorly and posteriorly on either side; tergite VIII with a small spine comb and a pair of fine hairs posteriorly on either side; segment IX without spine comb, tapered posteriorly, with slightly curved terminal spines, other setae simple, long and curved; sternite III with 2+2 anteriorly directed recurved hooks; sternite IV with 5+5 anteriorly directed recurved hooks; sternite V with 6+6 anteriorly directed recurved hooks, sternite VI with 2+2 anteriorly directed recurved hooks, sternite VII with 1+1 anteriorly directed recurved hooks, sternite VIII with a single hair on either side.



FIGURES 20–23. *Austrocnephia aurantiaca* male. (20) Antenna. (Brindabella). Scale bar = 0.1 mm. (21). Maxillary palp and lacinia. Paratype. (Mount Farrell, Tasmania). Scale bar = 0.1 mm. (22) Wing veins. Arrow indicates R_{2+3} . (Brindabella). Scale bar = 0.1 mm. (23) Claws and grappling hooks (g h). (Brindabella). Scale bar = 0.02 mm.

Cocoon. A closely fitting shapeless sac covering abdomen and variable proportions of the thorax, head and gills; silk fibers thick (Fig. 34), some markedly so, often with extraneous material incorporated.

Larva (based on numerous last instar larvae, multiple localities). **Body** (Figs. 36, 37): total length various, mainland populations 8.6–10.1 mm, Tasmanian populations 5.8–7.1 mm; evenly expanded from anterior to posterior abdomen; colour varied, from mottled brown, darker posteriorly, to evenly yellowish brown, or greenish, to pale (particularly for Tasmanian populations). **Head** (Fig. 38): evenly dark brown to light mottled brown, apotome slightly lighter than genae; head spot pattern weakly developed, tending to negative; length 0.87–1.2 mm, maximum width 0.71–0.78 mm; distance between antennal bases 0.44–0.48 mm; head widest just posterior to stemmata, narrowed irregularly anteriorly, convex posteriorly; cervical sclerites variously developed, fused to postocciput. **Antenna** (Fig. 39): short, apex not extended to end of labral fan stem; total length 0.33–0.36 mm, basal article unpigmented proximally, darker brown distally, medial article and distal articles evenly brown, basal article markedly shorter than medial article, proportional lengths of basal, medial and apical articles 1.0:1.5:1.2; medial article slightly expanded



FIGURES 24–27. *Austrocnephia aurantiaca* male. (24) Abdominal tergites (t) and sternites (st). Paratype. (Mount Farrell, Tasmania). Scale bar = 0.5 mm. (25) Genitalia (ventral view). Note downturned apex of ventral plate. (Carisbrook). Scale bar = 0.5 mm. (26) Gonocoxa (gc) and gonostylus (gs). Paratype. (Mount Farrell, Tasmania). Scale bar = 0.05 mm. (27) Slide mounted genitalia showing adeagal membrane (a m), basal arms (b a), parameres (p), spines (s) and ventral plate (v p). (Brindabella). Scale bar = 0.05 mm.

distally. *Labral fan*: stem short and broad, not markedly pigmented, unpigmented in early last instar larvae and in some last instar larvae, *ca.* 50 dark brown substantial rays, 10 posterior rays finer than others, length 1.0 mm, mid-ray width 0.01 mm; no conspicuous microtrichial pattern—most of similar length with longer ones (0.02 mm) at irregular intervals. *Mandible* (Figs. 40, 41): short and darkly pigmented; brushes well expressed; outer teeth short; apical tooth moderately developed; subapical teeth small and subequal in length; *ca.* six spinous teeth, the two distal teeth markedly expressed; serration various, not markedly developed; two sensilla present on slightly convex base; blade region short and convex. *Maxilla* (Fig. 42): heavily pigmented; palp cone-shaped, 1.9× as long as basal width; hair tuft at base of palp markedly developed. *Hypostoma* (Figs. 44, 45, 46, 47): darkly pigmented; tooth 0 with apex extended anteriorly to about the same level as that of tooth 4, giving anterior margin of hypostoma a poorly

expressed trilobed appearance; tooth 1 closely associated with tooth 0; teeth 2 and 3 shorter and less prominent; tooth 4 longer and flanged; teeth 5–8 decreasing in prominence laterad of tooth 4; lateral serrations typically absent, rarely present in some populations; 4–6 substantial hypostomal setae on each side; ratio of hypostoma: postgenal bridge: postgenal cleft 1.0:1.6:0.7. *Postgenal cleft* (Fig. 43): shallow, conspicuously wider than deep, with irregular anterior margin; posterior tentorial pits small, rectangular; postgenal bridge lightly pigmented, contrasting with the darker-brown genae. *Thorax* (Fig. 48): yellowish; gill histoblast with 4–6 primary trunks visible, anterior one thickened with bifurcations showing, all directed ventrally then posteriorly to produce thick L-shaped lobe, filament tips paler and directed anterodorsally. *Prothoracic proleg*: well developed, hooks of two sizes, lateral plate with vertical portion well-developed and darkly sclerotized, giving plate an overall L-shaped appearance (Fig. 49); lappets typically absent, if present then shorter than apical article of proleg (Figs. 49, 50, 51). *Abdomen*: evenly expanded from anterior to posterior segments, not markedly expanded at segments VII & VIII; paler anteriorly, darker posteriorly; colour ranging from banded mottled yellowish brown, to yellow, or grey. *Rectal papillae*: three simple lobes. *Ventral tubercles*: absent. *Anal sclerite* (Figs. 52, 53, 54): anterior arms markedly flared, relatively lightly sclerotized; main body of sclerite with conspicuous hole posteromedially; posterolateral arms usually absent, but slightly expressed in some populations (e.g., Fig. 54); posteroventral arms narrower and more heavily sclerotized than anterior arms, of varied lengths; faintly expressed posteriorly directed extensions projecting from proximal base of each arm into the dorsal junction of hooks in circlet; numerous sensilla situated in membrane immediately anterior to arms (e.g., Fig. 53); membranous area between posteroventral arms and circlet of hooks with 12–14 campaniform organs (often as short stout trichoid setae). *Posterior circlet*: markedly developed and directed slightly ventrally, ca. 260 rows of hooks with 30–33 hooks per row (total ca. 8,320 hooks).



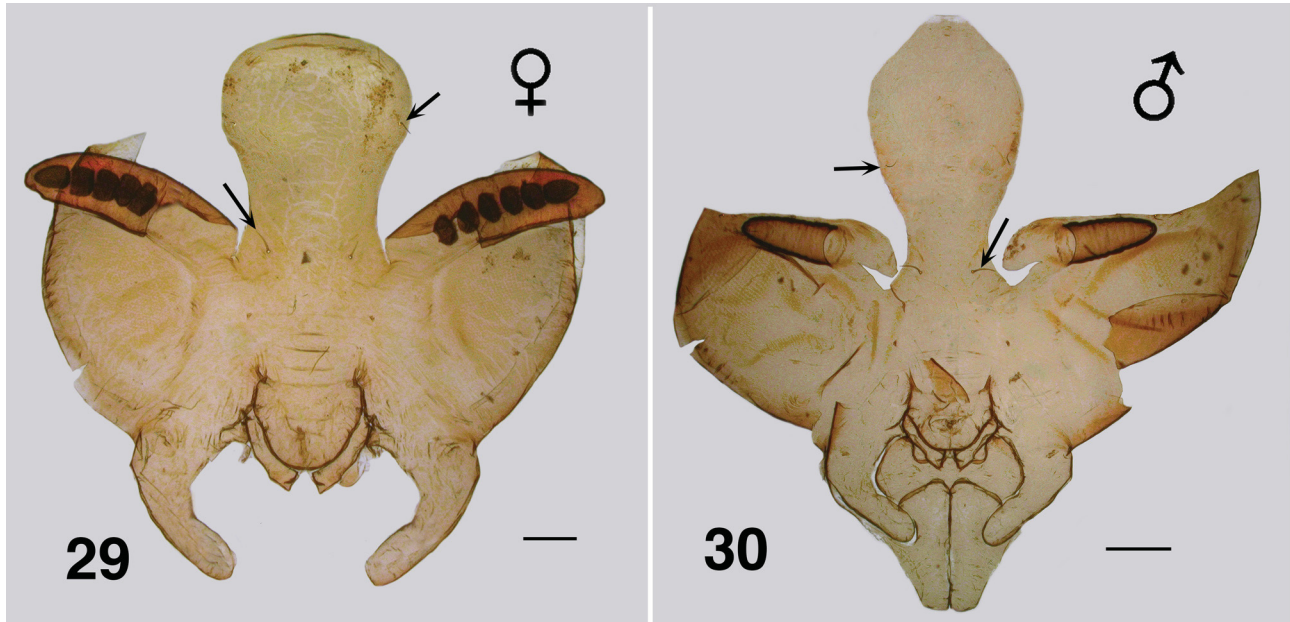
FIGURE 28. *Austrocnephia aurantiaca* pupa. (28) Habitus, male. (Carisbrook). Scale bar = 1.0 mm.

Etymology. Not given by Tonnoir, but no doubt in reference to the yellowish- orange adults.

Types. *Holotype*. Pinned female. NSW, Blue Mountains, Mount Wilson, S38.5000° E150.3700°. 19 Nov. 1921. Coll. Tonnoir. ANIC. Not examined. Exact labeling not recorded. Bugledich (1999: 327) listed the holotype plus 12 female paratypes in the ANIC, with two male paratypes in The British Museum (Natural History).

Paratypes. One was examined and photographed by LHG-A in 2007 (Fig. 1). Only four were found in ANIC by DAC (pers. obs.) in 2011. Two others are known (Daniels, 1978:416) from the Australian National Museum (Sydney), but were not examined:- Pinned female, label data:- [K.51170–*Cnephia aurantiacum*–Australia, New South Wales, Blue Mountains, Mount Wilson, (33° 30' 4" S , 150° 23' 41" E), 19 Nov. 1921, Paratype]. Pinned male, [K.51171–*Cnephia aurantiacum*–Australia, Victoria, Sassafras, (41° 17' S, 146° 30' E), 22 Oct. 1922, Paratype]. The following in ANIC: adults elbow-pinned (as for MacGillivray, 1903). Pinned male, [Tasm./Cradle Val./ 19 Jan. 1923/ A. Tonnoir] [(blue) PARATYPE/ (handwritten –*Simulium/ aurantiacum*)/ A. Tonnoir det.] [(green) Aust. Nat./ Ins. Coll.] [Examined by /D. A Craig/2013] [male symbol]. Condition—antennae absent, right wing with costa broken at half length, left fore- and mid-legs absent, other legs lacking tarsal claws and distal tarsomeres, otherwise

in good condition. (S41.6400° E145.9299°). Pinned female, label as for male plus [Examined by /D. A. Craig/2013] {♀}. Condition—head complete, apical half of left wing missing, left hind leg absent, right hind leg missing tarsus, right hind leg absent, overall good condition. Pinned female [Victoria/ Sassafras/ 22 Oct. 1922/ A. Tonnoir.], [(blue) PARATYPE/ (handwritten—*Simulium/ aurantiacum*)/ A. Tonnoir det.] [(green) Aust. Nat./ Ins. Coll.] [Examined by /D. A. Craig/2013] {♀}. Condition—poor, all extremities absent. Female, [Victoria/ Sassafras/ 22 Oct. 1922/ A. Tonnoir.], [(blue) PARATYPE/ (handwritten—*Simulium/ aurantiacum*)/ A. Tonnoir det.] [(green) Aust. Nat./ Ins. Coll.] [Examined by /D. A. Craig/2013] {♀}. Condition—good, left antenna and middle legs absent.



FIGURES 29, 30. *Austrocnephia aurantiaca* pupa. (29) Female cephalic capsule. (Brindabella). Arrows indicate setae. Scale bar = 0.2 mm. (30) Male cephalic capsule. (Brindabella). Scale bar = 0.2 mm.

Additional material examined. Two reared pinned adults with pupal exuviae in microvial—label data:- [*Austrocnephia aurantiaca*] [AUSTRALIA: Vic/ unnamed stream/ ex. M31 (Hume Fwy/ b/w Boho & Benalla/ 23 IX 1996/ {M}/ Coll. J.K. Moulton] [ANIC Database No./ 29 026637] and {F} [ANIC Database No./ 29 026636]. Seven pinned adults (two males, five female) with pupal exuviae in microvials—label data:- [*Austrocnephia aurantiaca*] [AUSTRALIA: VIC/ Steavenson Falls @/ Marysville/ S 31° 31.4'/E 145° 46.6'/ 21 September 1996/ Coll. J.K. Moulton] [ANIC Database No./ 29 026638–026644]. *Alcohol material:* Considerable material, largely collected by H. & P. Zwick, mainly of larvae and pupae [ANIC Database No./ 29 026540–026557; 29 026745–026843], [UASM#/ 352049, 352050, 352325, 353462, 353471–353475, 354121, 354123]. *Slide mounts:* All stages [UASM#/353349–3534621, 370732–370748, 370831].

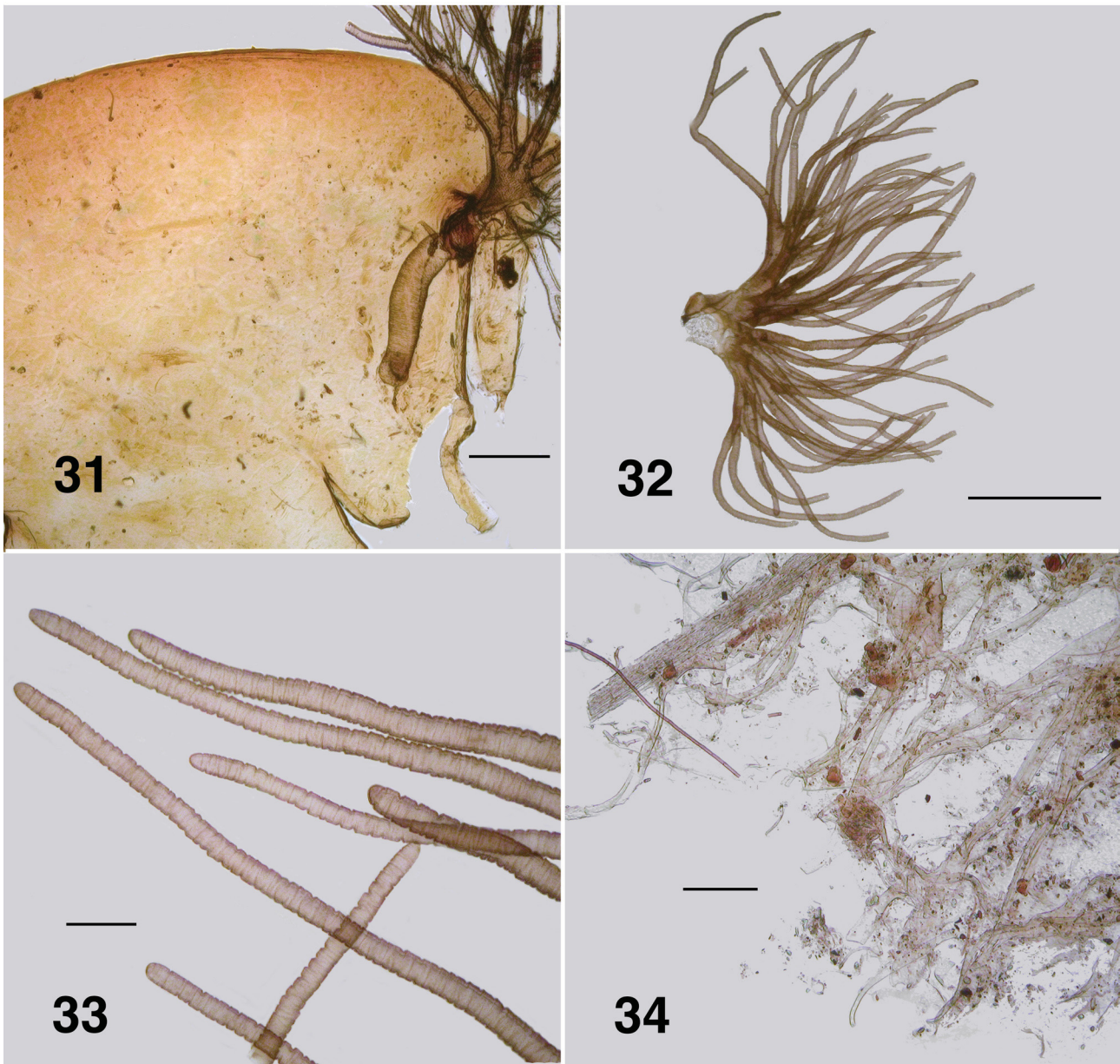
Bionomics. Tonnoir (1925: 236) noted that *A. aurantiaca* females had never been recorded as biting humans, even when occurring in considerable numbers. Mackerras & Mackerras (1949: 384) made the same observation. This is in agreement with the markedly small teeth on the mandible, but is at variance with distinct teeth on the lacinia and size of the CO₂ sensory vesicle (Lutz's Organ) on the maxillary palp (McIver, 1987; Sutcliffe *et al.*, 1987). A similar suite of character states is discussed by Craig *et al.* (2012) in regard to non-biting behaviour of *Austrosimulium* females in New Zealand. Given that *A. aurantiaca* females possess a distinct basal tooth on the claw (Fig. 11), perhaps they are strictly ornithophilic?

Label data from the extensive Zwick collection indicates that for higher altitude localities in NSW, water temperatures ranged from 8.0°C to 20.0°C, between July to January. For VIC, temperatures were from 6.0°C to 16.0°C, between May to February; in Tasmania, 11.5°C to 17.5°C during December. For localities known at the time, Mackerras & Mackerras (1949: 384) give dates of collection from October to February.

The majority of habitats comprise clear, fast-flowing streams and rivers (Fig. 57). Tonnoir (1925: 236) provides details of habitats visited by him. Mackerras & Mackerras (1949: 384) similarly note that *A. aurantiaca* is mainly associated with clear mountain streams. Using unpublished notes of Tonnoir's they reported that he considered it to be an uncommon species, with larvae found in isolation and pupae in clusters, typically on moss and less often

on stones. This is in agreement with habitat details included with the Zwick collections of this species. More recent collections, however, show that larvae can be found clustered in large numbers. Velocity determinations were made during the current investigation using the stand-pipe technique, also known as the head-tube technique (Craig, 1987b: 178. Ciborowski, 1991: 110). The water velocities recorded by us for *A. aurantiaca* immatures ranged from 0.8–1.1 m/s.

Tonnoir (1925: 219) observed that the following species co-occur with *Austrocnephia aurantiaca* in Tasmania: *Austrosimulium* (*A.*) *cornutum* Tonnoir, *A. (Novaustrosimulium) furiosum* (Skuse) (as *simile*), *A. (N.) victoriae* (Roubaud) (as *tasmaniense*) and *A. (N.) torrentium* Tonnoir. Blephariceridae have been recorded from *A. aurantiaca* habitats collected by H. & P. Zwick in 1977, 1981 & 1998. We have also occasionally encountered blepharicerid larvae in *A. aurantiaca* habitats—an indication of the high-velocity of breeding sites.



FIGURES 31–34. *Austrocnephia aurantiaca* pupa. (31) Female thoracic cuticle. (Steavenson Falls). Scale bar = 0.2 mm. (32) Gill. (Carisbrook). Scale bar = 0.5 mm. (33) Gill filament apex surface. (Carisbrook). Scale bar = 0.05 mm. (34) Cocoon silk. (Brindabella). Scale bar = 0.1 mm.

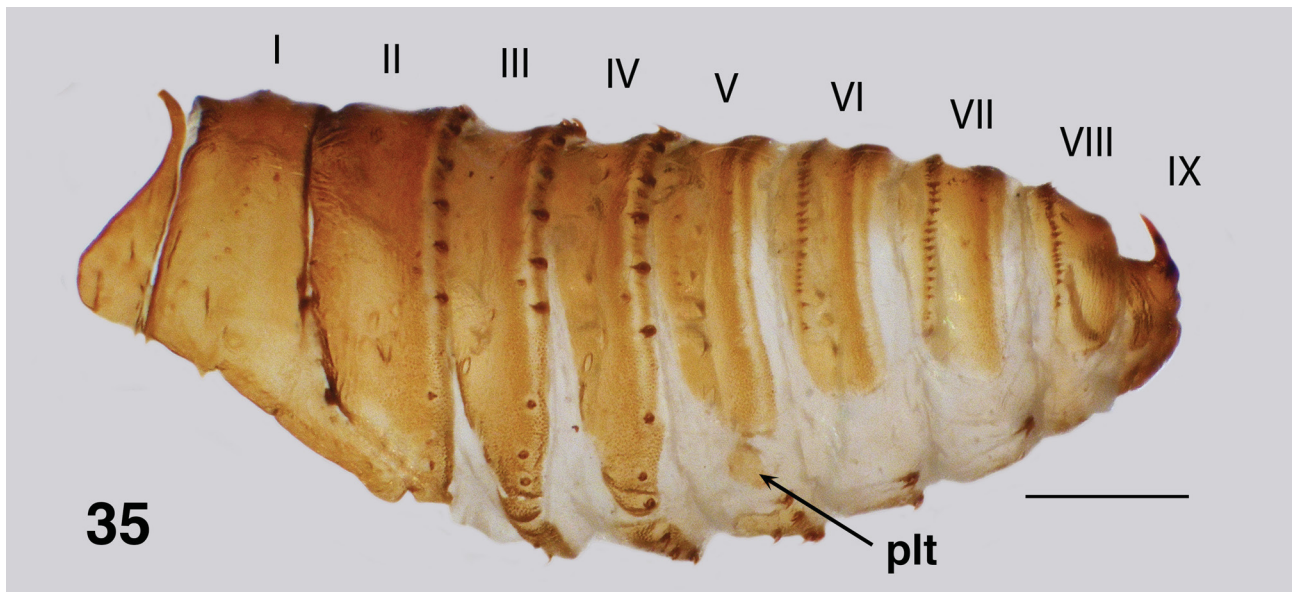
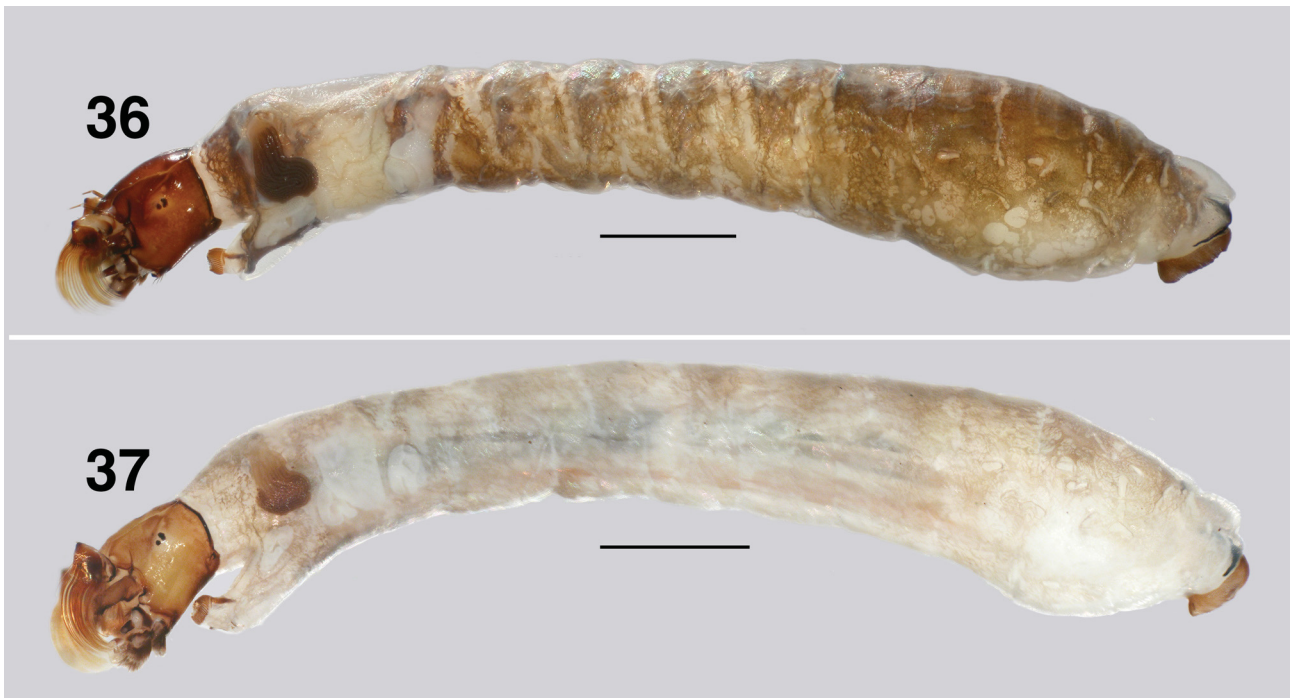


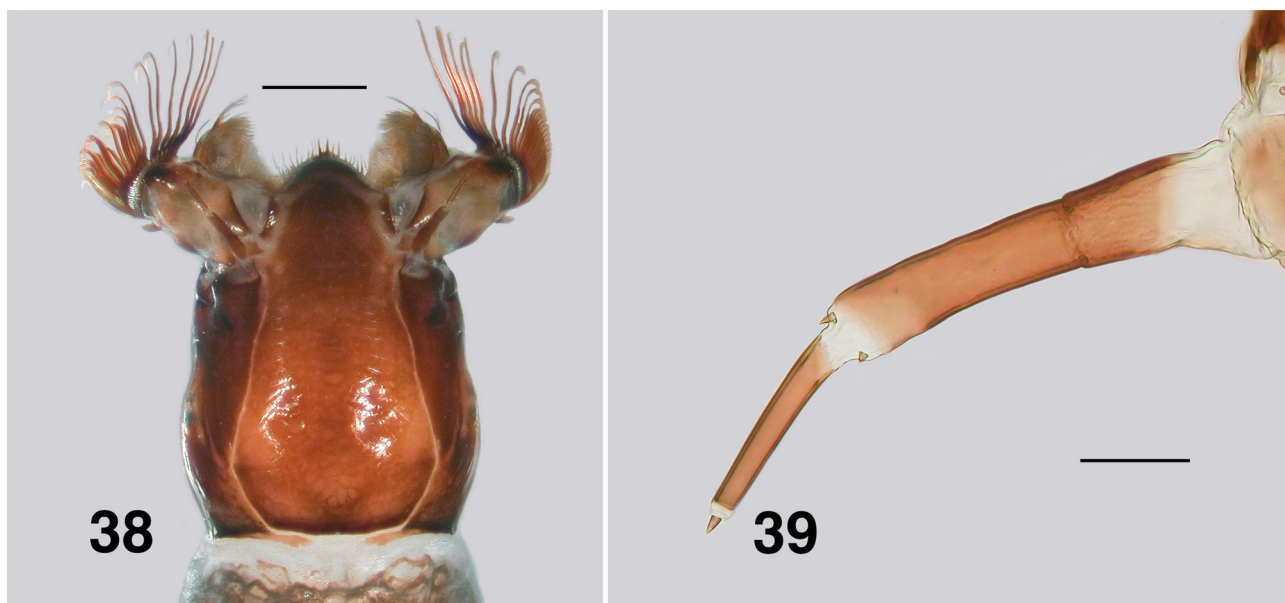
FIGURE 35. *Austrocnephia aurantiaca* pupa. (35) Abdominal armature. (Brindabella). Arrow indicates pleurite (plt). Scale bar = 0.5 mm.



FIGURES 36, 37. *Austrocnephia aurantiaca* larva. (36) Habitus, last instar. (Steavenson Falls). Scale bar = 1.0 mm. (37) Habitus, last instar. (Hogarth Rivulet, Tasmania). Scale bar = 1.0 mm.

Of the large number of simuliid samples examined by us, only two localities, Godfreys Creek (NSW, 11 Oct. 1972. Zwick) and Bellell Creek (Highway C153, NSW, Sept. 2014. Craig), yielded each a single parasitized larva. The organism appears as tightly packed spheres (dia. 0.03–0.05 mm) in the abdominal cavity (Fig. 55); similar to that shown by Adler *et al.* (2004; their Fig. 6.2). Examination at higher magnification reveals that the spheres have a refractive wall and fine grained contents (Fig. 56). It appears to be the Blastocladales (previously known as a Chytridiales fungus), *Coelomycidium simulii* Debais 1919. That species is known too for New Zealand *Austrosimulium* larvae (Craig *et al.*, 2012: 33, 294), similarly from cold water, as was the Bellell Creek locality. The organism may, however, possibly be the protist, *Tetrahymena* sp. (Adler *et al.*, 2004: 92). As far as is known, this is the first record of such an organism from an Australian simuliid. Litchwardt & Williams (1990) discuss trichomycete gut fungi of

Australian simuliid larvae and trichomyctes are now known for *Bunyipellum gladiator* (Moulton *et al.*, 2004: 8) and *Ectemnoides* (Moulton *et al.*, 2018: 45).

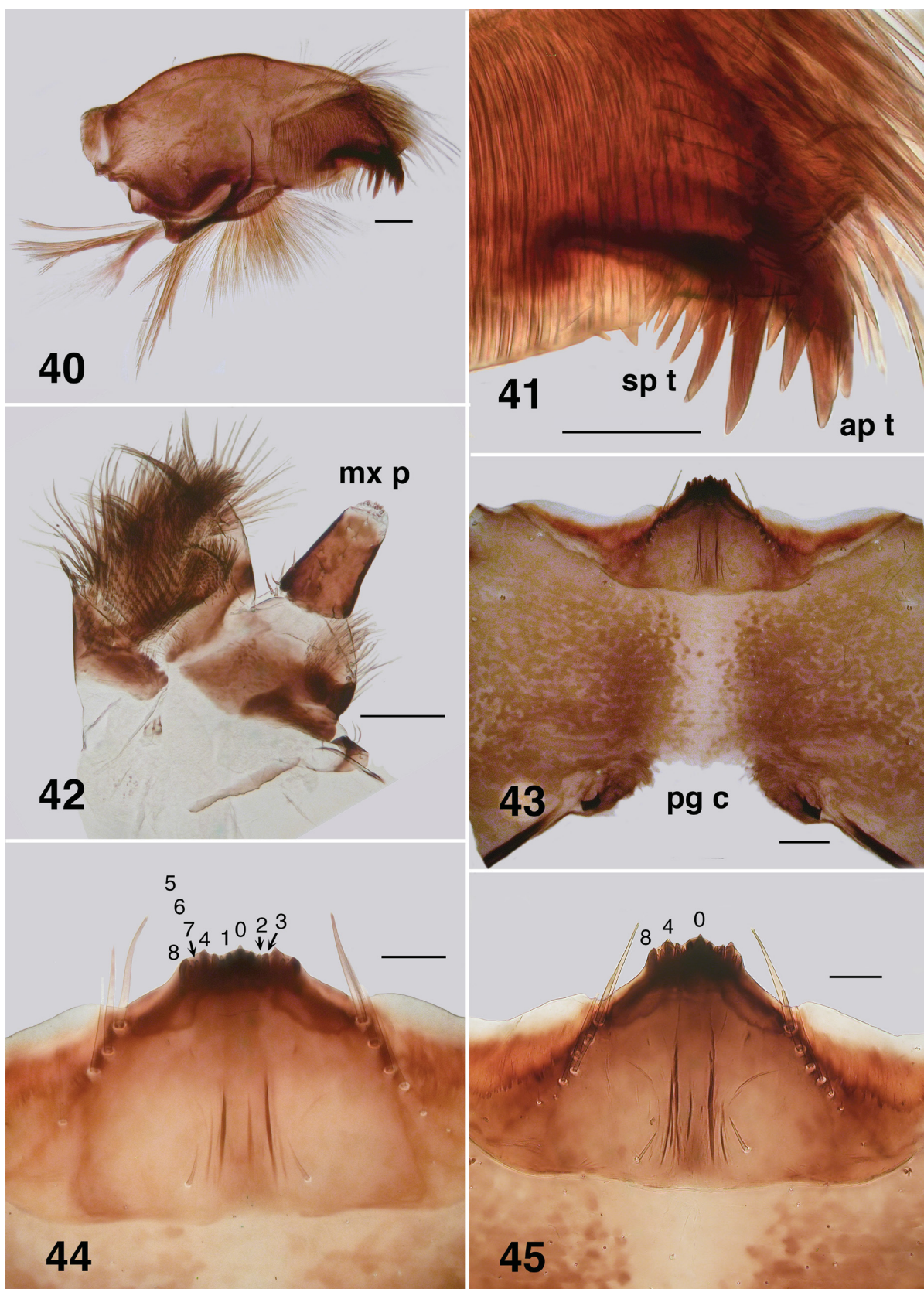


FIGURES 38, 39. *Austrocnephia aurantiaca* larva. (38) Dorsal view of head, last instar. (Steavenson Falls). Scale bar = 0.25 mm. (39) Antenna. (Steavenson Falls). Scale bar = 0.05 mm.

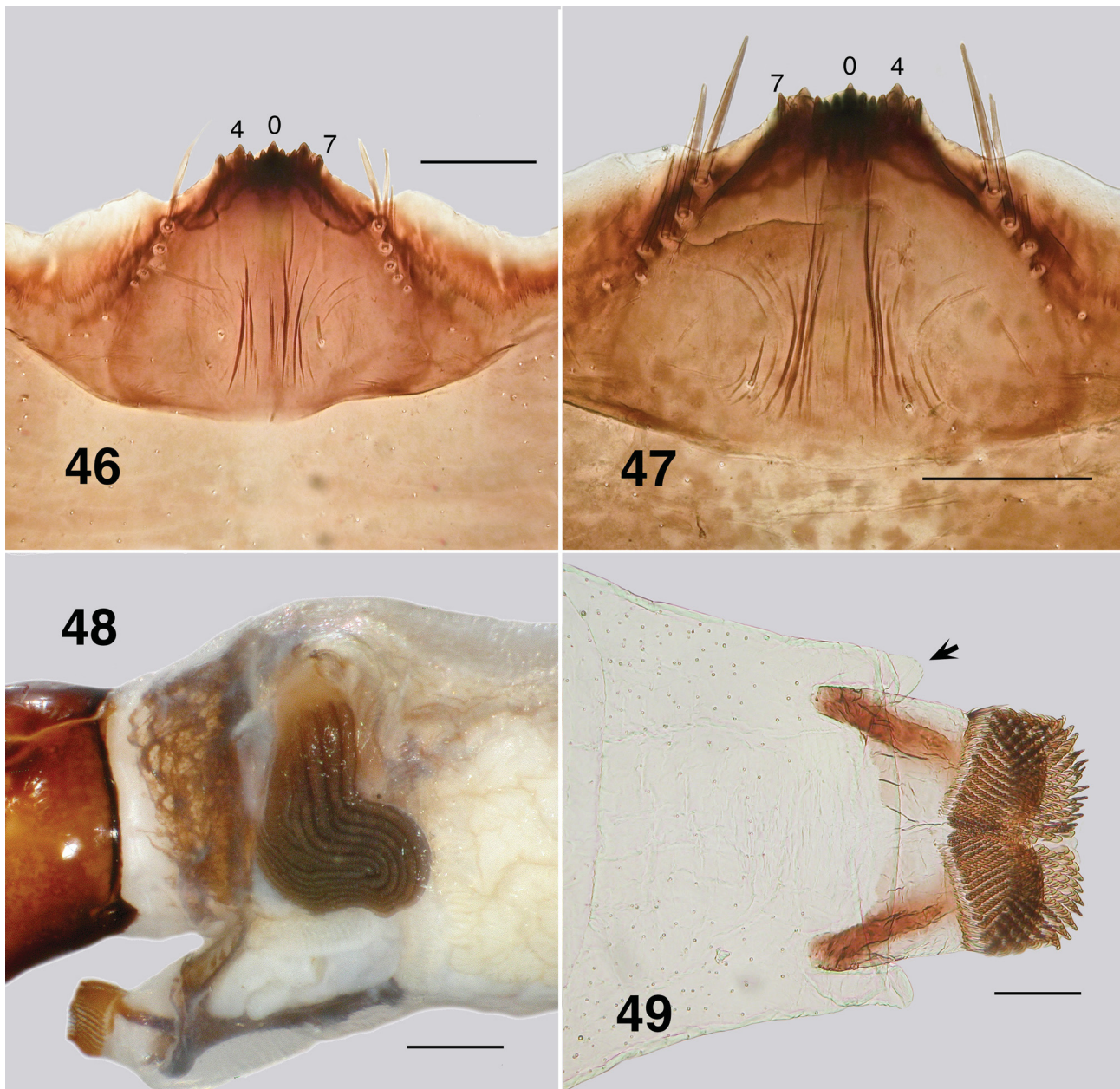
Distribution (Fig. 196). This is a widely distributed species, ranging from Queensland to Tasmania and south-west to the Grampians National Park and the Otway Range, Victoria.

Queensland: Mt. Bartle Frere, Josephine Falls, S17.4420° E145.8600°. 27 Oct. 2002. Adults. Coll. Zwick (ANIC). Mt. Spec, NW Townsville, S18.9500° E146.1800°. 22 Apr. 1955. Adult. Coll. Norris & Common (ANIC). Little Nerang Creek, near Gold Coast, S28.1800° E153.2700°. 10 Aug. 1948, 16 Aug. 1950. Adults. Coll. Unknown (ANIC). Springbrook, Twin Falls (Little Nerang) Creek, S28.1896° E153.2710°. 23 Jun. 1971. Larvae, pupae, reared adults. Coll. M.H. Colbo (ROM). Springbrook, Purling Brook Creek, S28.1898° E153.2709°. 9 Nov. 1973. Larvae. Coll. M.H. Colbo (ROM). Carnarvon Gorge National Park, Moss Garden & Hell Hole Gorge, S25.0550° E148.2250°. 13 Feb. 1997. Larva, pupae. Coll. Zwick (ANIC). Lamington Plateau, Elabana Falls, S28.1500° E153.0859°. 26 Dec. 1954. Coll. Mackerras (ANIC). Wilson's Peak, Teviot Brook, S28.2500° E152.4800°. 27 Apr. 1971. Larvae. Coll. M.H. Colbo (ROM).

New South Wales: Mt. Ebor, Gooch's Water, S30.4000° E152.3400°. 30 Sept. 1950. Reared male. 28 Sept. emerged 2 Oct. Reared female. Coll. Unknown (ANIC). New England National Park, S30.5800° E152.4600°. 12 Nov. 1961. Coll. I.F.B. Common & M.S. Upton (ANIC). Tubrabucca Falls, S31.8833° E151.4166°. 16 Nov. 1953. Females. Coll. Neboiss (ANIC). Barrington Tops, Upper Allyn River, near Whiterock campground, S32.1700° E151.500°. 24 Feb. 2001. Female. Coll. Zwick (ANIC). Williams River, S32.4064° E151.7605°. 7 Mar. 1953. Larvae, pupae. Coll. B. McMillan (UASM). Newcastle, S32.9300° E151.7800°. Male, female. Coll. Unknown (UASM). Crown Creek, S33.1800° E150.1100°. 14 Nov. 1971. Larvae. Coll. Hynes (ANIC). Crown Creek, Woods Pl, S33.1818° E150.1179°. 11 Oct. 1972. Larva, pupae. Coll. Zwick (ANIC & Australian National Museum [K51170]). Mt. Wilson, S33.5000° E150.3700°. 19 Nov. 1921. Larvae, female. Coll. A.L. Tonnoir (ANIC). Govetts Leap Creek, Bridal Veil Falls, S33.6333° E150.3129°. 18 Oct. 2014. Larvae. Colls. D.A. & R.E.G. Craig (ANIC, UASM). Wentworth Falls, S33.7274° E150.3742°. 18 Nov. 1921. Male. Coll. A.L. Tonnoir; 22 Nov. 1953. Male. Coll. Neboiss (ANIC). Jenolan Caves, S33.8200° E150.0500°. Coll. J. C. Wiburd. Mackerras & Mackerras (1949): Janolan Caves River, below Blue Lake, S33.8202° E150.0269°. 20 Oct. 2014. Larvae. Colls. D.A. & R.E.G. Craig (ANIC, UASM). Godfreys Creek, S34.1160° E148.7000°. 2 Apr. 1972, 11/12 Oct. 1972. Larva, pupae. Coll. Zwick (ANIC). Minnamurra Falls, near Wollongong, S34.6330° E150.7160°. 20 Feb. 2001. Larvae, pupae. Coll. Zwick & Theischinger (ANIC). Fitzroy Falls, S34.6470° E150.4825°. 22–27 Nov. 1937. Male. Coll. A.L. Tonnoir (ANIC). Pierce Creek State Forest, creek en route to Vanity Crossing, S35.3372° E148.9152°. 11 Oct. 2014. Larvae. Colls. D.A. & R.E.G. Craig (ANIC, UASM). Brindabella, Bramina Creek, S35.3835° E148.7410°. 10 Oct. 2011, 4 Oct. 2014. Larvae, pupae, reared adults. Colls. D.A. & R.E.G. Craig (ANIC, UASM). Geehi River, S36.2800° E148.0300°. 9 Nov. 1961. Female.



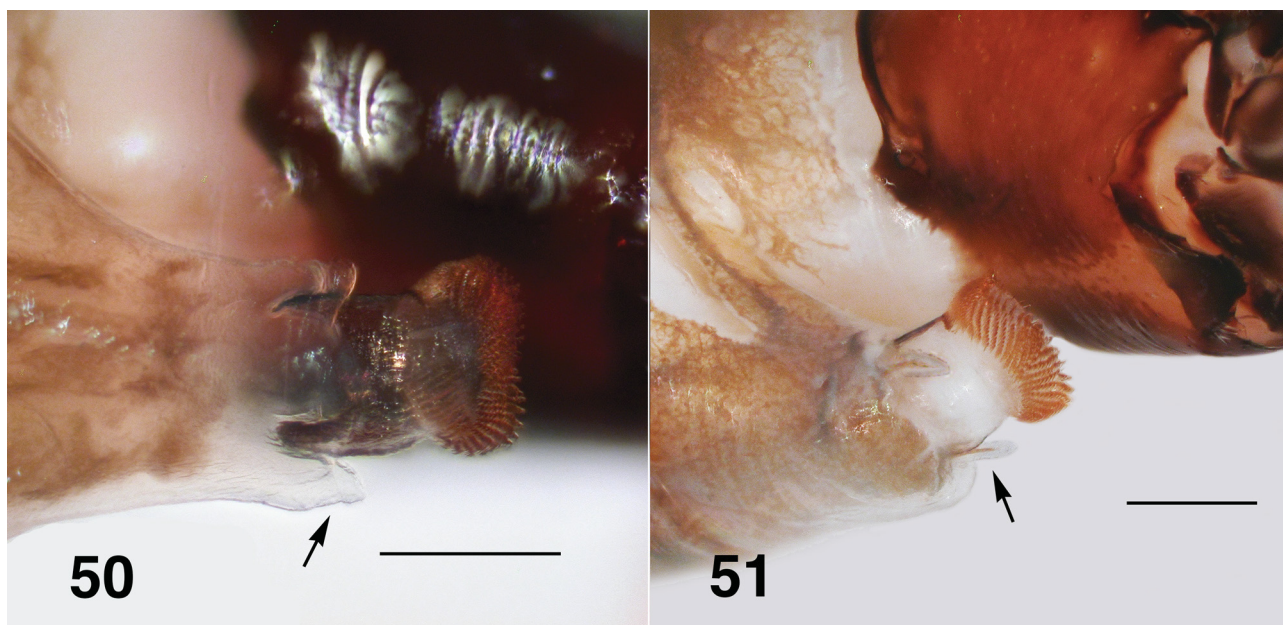
FIGURES 40–45. *Austrocnephia aurantiaca* larva. (40) Mandible. (Steavenson Falls). Scale bar = 0.05 mm. (41) Mandible apex showing apical tooth (ap t) and spinous teeth (sp t). (Pretty Valley). Scale bar = 0.05 mm. (42) Maxilla and palp (mx p). (Carisbrook). Scale bar = 0.1 mm. (43) Ventral head cuticle showing postgenal cleft (pg c). (Steavenson Falls). Scale bar = 0.1 mm. (44) Hypostoma. Numbers indicate teeth. (Steavenson Falls). Scale bar = 0.05 mm. (45) Hypostoma. (Carisbrook). Scale bar = 0.05 mm.



FIGURES 46–49. *Austrocnephia aurantiaca* larva. (46) Hypostoma. (Flinders Island). Scale bar = 0.1 mm. (47) Hypostoma. (Huon River, Kerranda, Tasmania). Scale bar = 0.1 mm. (48) Pupal gill histoblast. (Steavenson Falls). Scale bar = 0.25 mm. (49) Prothoracic proleg. Arrow indicates rudimentary lappet. (Steavenson Falls). Scale bar = 0.1 mm.

Coll. D. H. Colless (ANIC). Mt. Kosciuszko, Diggers Creek, S36.2800° E148.5100°. 11 Feb. 1924. Coll. Nicholson (ANIC). Mt. Kosciuszko, near Mare Creek, trib. Bogong River, S36.2800° E148.2300° 10 Nov. 2005. Larvae. Coll. Theischinger & Zwick (ANIC). Mt. Kosciuszko, Diggers Creek, below falls, S36.3377° E148.4891°. Larvae. Coll. Zwick (ANIC). Mt. Kosciuszko, Alpine Way, Bogong Creek, S36.3563 E148.2029. 17 Sept. 2006. Larvae. Coll. Zwick (ANIC). Mt. Kosciuszko, Geehi River, Alpine Way, S36.3800° E148.1800°. 4 Nov. 2007. Pupae. Coll. Zwick (ANIC). Kosciuszko, Pipers Creek, S36.3839° E148.4347°. 21 Nov. 1972, 4 Jan. 1973. Larvae, pupae. Coll. Zwick (ANIC). Pipers Creek, right falls, S36.3839° E148.4347°. 26 June 1972. Larvae. Coll. Zwick (ANIC). Mt. Kosciuszko, Snowy River, island, S36.4000° E148.0000°. Aug. 1972. Larvae. Coll. Zwick (ANIC). Mt. Kosciuszko, Guthrie's Creek, S36.4300° E148.3200°. 22 Nov. 1972. Larvae. Coll. Zwick (ANIC). Mt. Kosciuszko, Snowy River, Charlottes Pass, S36.4302° E148.3222°. 22 Nov. 1972, 5 Jan. 1973. Larva, pupae. Coll. Zwick (ANIC). Mt. Kosciuszko, Threadbo River, S36.5000° E148.3000°. 22/23 Oct. 1972. Larva, pupae. Coll. Zwick (ANIC). Brown Mountain, February 1939. Coll. Unknown (ANIC). Brown Mt., Rutherford Creek, S36.5650° E149.4511°. 10 Mar.

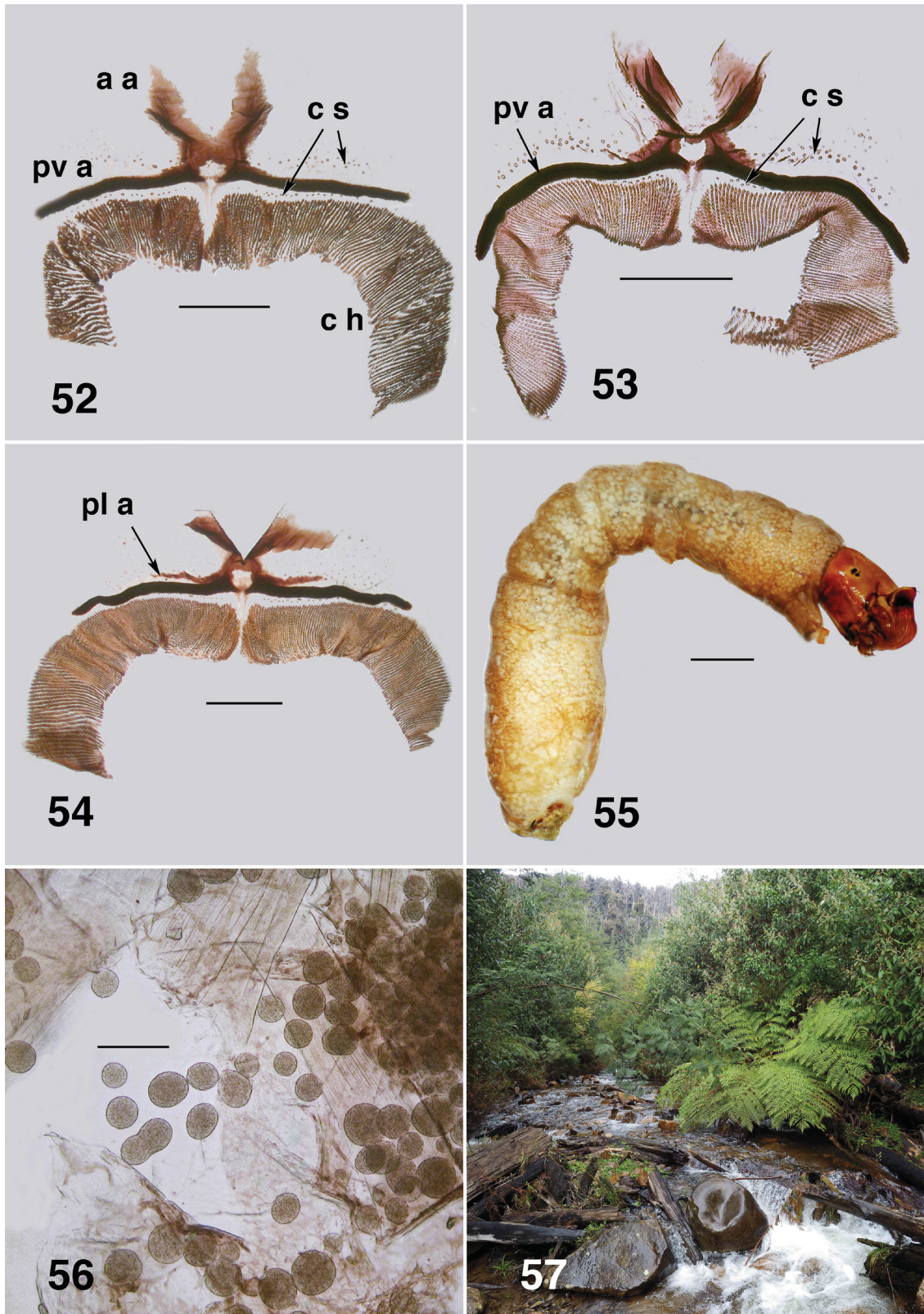
1961. Male. Coll. D.H. Colless (ANIC). Brown Mountain, Rutherford Creek, S36.5800° E149.5500°. 10 Mar. 1969. Coll. D.H. Colless (ANIC).



FIGURES 50, 51. *Austrocnephia aurantiaca* larva. (50) Prothoracic proleg. Arrow as for Fig. 49. (Steavenson Falls). Scale bar = 0.25 mm. (51) Prothoracic proleg, Arrow as for Fig. 49. (Steavenson Falls). Scale bar = 0.2 mm.

Australian Capital Territory: Blundell's, S35.2900° E149.1400°. October. Coll. A.L. Tonnoir (ANIC). Cotter River, bridge, S35.3228° E148.9504°. Larvae. Coll. Zwick (ANIC). Coree Creek, S35.3300° E148.8800°. 21 Jan. 1931. Coll. Unknown. Det. A.L. Tonnoir (ANIC). Paddy's River, S35.3600° E148.9500°, 30 Sept. 1962. Coll. Unknown (ANIC). Namadgi Nat. Park, Gibraltar Falls, S35.4897° E148.9293°. Larvae. 8 Oct. 2002. Coll. Zwick (ANIC). Namadgi Nat. Park, Bushrangers Creek, S35.4156° E148.8313°, 8 Oct. 2002. Pupae. Coll. Zwick (ANIC). Gibraltar Creek Falls, S35.4871° E148.9345°. 26 Aug. 1972. Larvae. Coll. Zwick (ANIC). Mt. Gingera, Snowy Flats Creek, S35.5000° E148.8166°. Coll. Unknown (ANIC).

Victoria: Omeo Hwy, Lightning Creek, S36.6800° E147.4400°. 13 Apr. 1972. Larva, pupae. Coll. Zwick (ANIC). Tawonga, S36.7000° E147.1000°. 16 May 1972. Larva, pupae. Coll. Zwick (ANIC). Mt. Buffalo, Eurobin Creek, downstream falls on crossing, S36.7171° E146.8421°. 12 April. Pupae. 7 Nov. 2005. Males. Coll. Zwick (ANIC). Mt. Buffalo, Eurobin Creek and Falls, S36.7199° E146.8365°. 13 Apr. 1972, 24 Nov 1972, 10 Oct. 2002. Larva, pupae. Coll. Zwick (ANIC). Mt. Stirling, headwater stream, N of summit on Circuit Rd, S36.7300° E147.2800°. 23 Nov. 2005. Larva, pupae. Coll. Zwick (ANIC). Slippery Rock Creek, Mt. Beauty Falls, S36.7330° E147.1600°. 14 Apr. 1972. Larvae. Coll. Zwick (ANIC). Mt. McKay, Pretty Valley, Howmans Gap, stream, S36.8330° E147.2500°. 7 Jan. 1973. Larvae, pupae, adults. Coll. Zwick (ANIC). Falls Creek, west bank, S36.8633° E147.2802°. 7 Jan. 1973. Larva, pupae. Coll. Zwick (ANIC). Mt. Ben Cairn, Myrtle Creek, S36.9500° E144.4200°. 7/9 Oct. 1972, 25 Dec. 1972. Larva, pupae, males. Coll. Zwick (ANIC). Mansfield, Mt. Buller, Chalet Creek, S37.1200° E146.4400°. 6 Nov. 2005. Larvae. Coll. Zwick (ANIC). Mansfield, Mt. Stirling, S37.1200° E146.4400°. 23 Nov. 2005. Larvae, pupae. Coll. Zwick (ANIC). Mirimbah, Mt. Buller, Delatite River, S37.1098° E146.397°. 17 Feb. 2001. Larva, pupae. Coll. Zwick (ANIC). Mirimbah, Delatite River, S37.1098° E146.3982°. 11 June 1972, Feb. 1987. Larva, pupae. Coll. Zwick (ANIC). Mirimbah, Buller Creek, S37.1333° E146.4166°. 1 Sept. 1972, 24 Nov. 1972. Larvae, pupae. Coll. Zwick (ANIC). Mansfield, Delatite River, S37.1389° E146.1690°. 20 Dec. 1972, Jan. 1987, 06 Nov. 2005. Larvae, pupae. Coll. Zwick (ANIC). Mt. Buller, white bridge, S37.1400° E146.4400°. 11 Apr. 1972, 20 Dec. 1972, 8 Jan. 1973, 17 Feb. 2001. Larvae, adults. Coll. Zwick (ANIC). Mt. Buller, Chalet Creek, S37.1400° E146.4400°. 17 Feb. 2001. Larvae, pupae, adults. Coll. Zwick (ANIC). Mansfield, Mt. Stirling, Bindaree Falls, S37.1490° E146.5562°. 23 Nov. 2005. Larvae, pupae. Coll. Zwick (ANIC). Buller Creek, S37.1500° E146.4400°. 2 Oct. 1972. Larvae, pupae. Coll. Zwick (ANIC). Howgaa River, Stockyard Flats, S37.2200° E146.1800°. 15 Apr. 1972. Larvae, pupae. Coll. Zwick (ANIC). Eildon Lake, Fryers Creek, S37.3456° E146.0703°. 3 Oct. 1972. Larvae. Coll. Zwick (ANIC). Big River, Lake Eildon, S37.2300° E145.9700°. 3 Dec. 1972, Feb. 1987. Larvae, pupae. Coll. Zwick (ANIC).



FIGURES 52–56. *Austrocnephia aurantiaca* larva. (52) Larval anal sclerite and circlet of hooks showing anterior arm (a a), posteroventral arms (pv a), campaniform sensilla (c s), circlet of hooks (c h). (Carisbrook). Scale bar = 0.2 mm. (53) Anal sclerite and circlet of hooks. (Flinders Island). Scale bar = 0.2 mm. (54) Anal sclerite and circlet of hooks, showing posterolateral arms (pl a). (Pretty Valley). Scale bar = 0.2 mm. (55) Parasitized larva. (Godfreys Stream, NSW). Scale bar = 0.5 mm. (56) *Coelomycidium* (?) *simulii*. (Godfreys Stream, NSW). Scale bar = 0.1 mm. **FIGURE 57.** *Austrocnephia aurantiaca* typical habitat. (57) Steavenson River, NSW. 24 Sept. 2014.

Taponga River, Eildon Lake, S37.3700° E146.0500°. 11 June 1972, 17 Dec. 1972. Larvae. Coll. Zwick (ANIC). The Grampians, Mackenzie River, McKenzie Falls, S37.1109° E142.4087°. 30 Sept. 1954, Larvae. Coll. Neboiss (ANIC), 27 Sept. 1996, Larvae, pupae. Coll. J. K. Moulton (JKM, UASM). Grampians, Halls Gap, Fyans Creek, nr Mt. Williams Road, S37.2390° E142.5370°. 11 Nov. 1972. Larvae, pupae. Coll. Zwick (ANIC). Mt. Cole, 20 ml S. Ararat, Ferntree Falls, S37.3100° E143.2400°. 8 Nov. 1972. Larvae. Coll. Zwick (ANIC). Jamieson River, S37.2700° E146.1330° 3 Oct. 1972. Larvae, pupae. Coll. Zwick (ANIC). Baker Creek, Jamieson, S37.3000° E146.1400°. 28 Apr. 1972. Larvae, pupae. Coll. Zwick (ANIC). Snobbs Creek Falls, S37.3000° E145.8800°. 9 Nov. 1972, 19 Dec. 1972, 28 Dec. 1972, 6 Feb. 1973. Larvae, pupae. Coll. Zwick (ANIC). The Grampians, Kalymna Falls, S37.3229° E142.6187°. 9 Nov. 1972. Larvae, pupae, adults. Coll. Zwick (ANIC). Royston River, S37.3833° E145.8833°. 28 Dec. 1972. Larvae, pupae. Coll. Zwick (ANIC). Flourbag Creek, Jamieson, S37.3840° E146.2120°. 28 Apr. 1972. Larvae, pupae. Coll. Zwick (ANIC). Kinglake West, King Parrot Creek, S37.4283° E145.2496°. 18 Oct. 1953, 13 Dec. 1953. Male. Coll. Neboiss (ANIC). Taponga River, S37.4400° E146.0200°. 19 Dec. 1972. Larvae, pupae. Coll. Zwick (ANIC). Gaffneys Creek, Woods Point Road, S37.4606° E146.1893°. 27 Jan. 1972, 11 Oct. 1972. Larvae, pupae. Coll. Zwick (ANIC). Kinglake, Masons Falls, S37.4900° E145.2480°. 13 Dec. 1953. Coll. Neboiss (ANIC). Marysville, Taggerty River, Lady Talbot Drive, S37.5045° E145.7957°. 21 Nov. 2005. Female. Coll. Zwick (ANIC). Narbethong, Acheron River, S37.5284° E145.6884°. Larvae, pupae. Coll. Zwick (ANIC). Marysville, upper Big River, Cumberland Rd, S37.56200° E145.9035°. 22 Nov. 2005. Pupae. Coll. Zwick (ANIC). Marysville, Steavenson Falls, S37.5317° E145.7727°. 26 Apr. 1972, 11 June 1972, 8 Sept. 1972, 4 Nov. 1972, 29 Dec. 1972. Larvae, pupae. Coll. Zwick (ANIC) Marysville, Steavenson River, turbine house, Steavenson Falls, S37.53144° E145.7728°. 24 Sept. 2014, 22 Oct. 2014. Larva, pupae. Colls. D.A. & R.E.G. Craig (ANIC, UASM). Healesville, Myer's Creek, S37.5900° E145.5100°. 16 Jul. 1972. Larvae. Coll. Zwick (ANIC). Marysville, Keppel Falls, S37.6004° E145.8391° Feb 1987. Larvae, pupae. Coll. Zwick (ANIC). Marysville, Cumberland Falls, S37.6300° E145.7700°. 11 June 1972, 28 Dec. 1972. Larvae, pupae. Coll. Zwick (ANIC). Acheron River, Acheron's Gap, S37.6800° E145.7500°. 20 Apr. 1972. Larvae. Coll. Zwick (ANIC). Warburton, Cement Creek, S37.7239° E145.7542°. 2 Feb. 1972, 4 Feb. 1972, 1 Mar. 1972, 4 July 1972, 7 Oct. 1972, 8 Nov. 1972, 25 Dec. 1972, 20 Nov. 2005. Larvae, pupae, female. Coll. Zwick (ANIC). Dandenong Range, Barbers Road, Olinda Creek, S37.8290° E145.3763°. 26 Oct. 2014. Larva, pupae. Colls. D.A. & R.E.G. Craig (ANIC, UASM). Noojee, Torongo Fall, S37.8481° E146.0512°. 3 Jan. 1973. Female. Coll. Zwick. ANIC. Baw Baw, East Tanjil River, S37.8590° E146.1873°. 18 Nov. 2005. Larvae, pupae. Coll. Zwick (ANIC & Australian National Museum [K51171]). Sassafras, S37.8600° E145.3500°. October. A.L. Tonnoir (1925) (ANIC). Mt. Dandenong, Sherbrooke Falls, S37.8874° E145.3513°. October. A.L. Tonnoir (1925). 7km W Neerim, Torago River, S37.9500° E145.8900°, 1 March. 1972. Adult. Coll. Neboiss (MM). German Creek, S37.9851° E146.1496°. 23 Nov. 1972. Larvae, pupae. Coll. Zwick (ANIC). Gippsland, North of Moe, Tyers River, S38.1600° E146.2400°. 17 Nov. 2005. Larvae, pupae. Coll. Zwick (ANIC). Otway Ranges, Carisbrook Creek Falls, S38.6876° E143.8101°. 18 Aug. 1972, 13 Oct. 2002. Larvae, pupae, male. Coll. Zwick (ANIC). Great Ocean Road, Carisbrook Creek, bridge, S38.6909° E143.8092°. 20 Nov. 2011. Larvae. Colls. D.A. & R.E.G. Craig (ANIC, UASM). Great Ocean Road, Smythe Creek, S38.7033° E143.7617°. 21 Nov. 2014. Larva, pupae. Colls. D.A. & R.E.G. Craig (ANIC, UASM).

Flinders Island (Bass Strait): Mt. Strezlecki, S40.2400° E148.0800°. Jan. 1953. Coll. R. Mykutowycz. Larvae (1 slide), pupae (ANIC).

Tasmania: Cradle Valley, S37.8600° E145.3500°. 19 Jan. 1923. A.L. Tonnoir (ANIC); Jan, February. (Mackerras & Mackerras 1949). Duck River, 6km SW Roger River, S41.0058° E145.0672°, 29 Nov 1974. Adult. Coll. Neboiss (MM). Roger River, Buffs Road, Roger River Road, S41.0432° E145.0172°, DUCK28. 16 Mar. 1995. Larvae. Coll. M. Nelson, DPIPWE (TMAG). Burnie, S41.0500° E145.8900°. Coll. Tonnoir (1925). Penguin, Penguin Creek, Hayward Street, S41.1139° E146.0690°, BLYT04. 5 Apr. 2006 Larvae. Coll. D. Horner, DPIPWE (TMAG). Meander River, Falls Road, S41.2307° E147.6098°, MEAN13. 14 Nov. 2002. Larvae. Coll. D. Horner, DPIPWE (TMAG). Hogarth Rivulet, end of Falls Road, S41.2307° E147.6098°, GFOR31. 19 Nov. 2002, 20 Mar. 2003, 7 Oct. 2003, 5 Oct. 2004, 19 Apr. 2005, 4 Nov. 2005, 1 Apr. 2009. Larvae. Colls. T. Krasnicki, D. Horner, S. Meyer, Latton, DPIPWE (TMAG). Mackenzie Valley Road, Mackenzie Rivulet, S41.2312° E147.5494°, GFOR35. 10 May 2005. Larvae. Coll. D. Horner, DPIPWE (TMAG). Wilmot River, Alma Reserve, S41.2606° E146.2323°, FORT06. 17 Mar. 2004. Larvae. Coll. A. Foley, DPIPWE (TMAG). Arthur River, Pykes Bridge, S41.2636° E145.5154°, ARTH01. 27 Oct. 2004. Larvae. Coll. A. Harvey, DPIPWE (TMAG). Great Forester River, off East Diddleum Road, S41.2670° E147.5070°, GFOR17. 6 Oct. 2003, 4 Oct. 2004, 8 Nov. 2005. Larvae. Colls. M. Read, S. Meyer,

D. Horner, T. Krasnicki, DPIPWE (TMAG). Hellyer River, S41.2700° E145.6100°. 2 Dec. 1972. Larvae, pupae. Coll. Zwick (ANIC). St. Patricks River, Corkerys Road, S41.2936° E147.4160°, NESK22. 29 Mar. 1995. Larvae. Coll. D. Oldmeadow, DPIPWE (TMAG). South George River, St. Columba Falls Road, S41.2981° E147.9572°, GEOR07. 30 Mar. 1995. Larvae. Coll. D. Oldmeadow, DPIPWE (TMAG). St. Patrick River, S41.3600° E147.3100°. Coll. Tonnoir (1925). Launceston Gorge, S41.4400° E147.1200°. 8 Dec. 1972. Larvae. Coll. Zwick (ANIC). Whyte River, Waratah Road, S41.4667° E145.3906°, PIEM02. 27 Oct. 2004. Larvae. Coll. J. Latton, DPIPWE (TMAG). Cradle Mt. road waterfall, near Celthana Dam, S41.4700° E146.1600°. 9 Dec. 1972. Larvae. Coll. Zwick (ANIC). Mersey River, upstrm of Union Bridge, S41.5100° E147.3300°, MERS06. 14 Nov. 2002. Larvae. Coll. D. Horner, DPIPWE (TMAG). Dove Lake, S41.6660° E145.9666°. 9 Dec. 1972. Pupae. Coll. Zwick (ANIC). Meander River, dwnstr dam site, S41.5200° E147.0300°, MEAN10. 22 Oct. 2003. Larvae. Coll. T. Krasnicki, DPIPWE (TMAG). Mersey River, Dogs Head Hill, S41.5210° E145.2870°, MERS07. 11 Nov. 2002. Larvae. Colls. D. Horner, C. Amos, DPIPWE (TMAG). Blythe River, South Riana Road, S41.5688° E147.2391°, BLYT01. 29 Oct. 2003. Larvae. Coll. A. Foley, DPIPWE (TMAG). Jackeys Creek, dwnstrm of Jackeys Marsh, S41.6716° E146.6467°, MEAN31. 19 Oct. 2006. Larvae. Coll. D. Spiers, DPIPWE (TMAG). Liffey River, upstm of Liffey, S41.6809° E146.9260°, MEAN16. 23 Oct. 2003, 18 Nov. 2005, 11 Oct. 2006. Larvae. Colls. A. Foley, T. Krasnicki, J. Beard, DPIPWE (TMAG). Forth River, waterfall, S41.6900° E146.0750°. 29 Jun. 1967. Adult. Coll. E. F. Riek. 10 Dec. 1972. Larvae. Coll. Zwick (ANIC). Mt. Farrell, S41.7500° E145.6300°. Coll. Tonnoir (1925). Fish River, Mersey Forest Road, S41.7714° E146.2251°, MERS34. 15 Nov. 2005. Larvae. Coll. T. Krasnicki, DPIPWE (TMAG). Stitt River, upstream of Roseberry, S41.7919° E145.5409°, PIEM22. 11 Apr. 1995. Larvae. Coll. M. Nelson, DPIPWE (TMAG). Mackintosh River, S41.8833° E145.8833°. 3 Dec. 1972. Larvae, pupae. Coll. Zwick (ANIC). Ewart Creek, Zeehan Highway, S41.9576° E145.4631°, HENT13. 29 Apr. 2003, 16 Mar. 2004, 26 Oct. 2004, 28 Mar. 2006. Larvae. Colls. J. Latton, A. Harvey, M. Read, D. Warfe, DPIPWE (TMAG). Queenstown, Ewarts Creek Road, S41.9941° E145.4716°. 3 Dec. 1972, 6 Dec. 1972. Larvae. Coll. Zwick (ANIC). Allens Rivulet, Kaoota Road, S42.0199° E147.1652°, HOBA15. 5 Oct. 2005. Larvae. Coll. J. Latton, DPIPWE (TMAG). Strahan, Botanical Creek, Hogarth Falls, S42.1498° E145.3479°. 4 Nov. 2014. Larvae. Colls. D.A. & R.E.G. Craig (UASM). Collingwood River, S42.1600° E145.9200°. 4 Dec. 1972. Larvae, pupae. Coll. Zwick (ANIC). Henry River, S42.2200° E146.0210°. 3 Dec. 1972. Pupae. Coll. Zwick (ANIC). Florentine River, Florentine Road, S42.4433° E146.5052°, UDER008. 16 Mar. 2004, 19 Oct. 2005, 16 Oct. 2006. Larvae. Colls. D. Horner, K. Hoyle, D. Spiers, DPIPWE (TMAG). Russell Falls, S42.6700° E146.7100°. Dec. 1922. Larvae, pupae. Coll. Tonnoir (UASM) Mt. Field Nat. Park, Lady Barron Falls, S42.6838° E146.7172°. 6 Dec. 1972. Larvae, pupae. Coll. Zwick (ANIC). Mt. Field Nat. Park, Russell Falls, S42.6841° E146.7199°. 5 Dec. 1972. Larvae, pupae. Coll. Zwick (ANIC). Mt. Field National Park, Lady Barron Creek, S42.6881° E146.6989°. 7 Nov. 2014. Larvae. Colls. D.A. & R.E.G. Craig (UASM). Mt. Field Nat. Park, Tyenna River, S42.7200° E146.6700°. 6 Dec. 1972. Larvae, pupae. Coll. Zwick (ANIC). Ferntree, nr Hobart, S42.9200° E147.2600°. 7 Dec. 1972. Larvae, pupae. Coll. Zwick (ANIC). North West Bay River, Betts Road, S42.9544° E147.2066°, HOBA02. 20 Apr. 2006. Larvae. Coll. D. Horner, DPIPWE (TMAG). North West Bay River, upstream of Allens Rivulet, S42.9818° E147.1996°, HOBA06. 21 Oct. 2005. Larvae. Coll. D. Horner, DPIPWE (TMAG). North West Bay River, Margate weir, S42.9893° E147.2214°, HOBA05. 28 Apr. 2006. Larvae. Coll. D. Horner, DPIPWE (TMAG). Hartz Mts., Huon River, S43.1600° E146.6900°. 6 Dec. 1972. Larvae, pupae. Coll. Zwick (ANIC). Kermandie River, Oigles Road, S43.1681° E146.8787°, HUON013. 24 Oct. 2003, 28 Sept. 2005. Larvae. Colls. D. Warfe, D. Spiers, DPIPWE (TMAG). Hartz Mts., Arve River, S43.2600° E146.8000°. 7 Dec. 1972. Larvae, pupae. Coll. Zwick (ANIC). Esperance River, Esperance River Road, S43.2774° E146.8765°, HUON046. 8 Apr. 2004, 12 Oct. 2006. Larvae. Colls. A. Harvey, D. Spiers, DPIPWE (TMAG). Bruny Island, S43.4000° E147.2600°. Coll. A.L. Tonnoir (1925).

Remarks. *Austrocnephia aurantiaca* is a highly variable species, as noted by Tonnoir (1925: 236) in his original description. Based on our examination of a large series of material from many localities, ranging from near Cairns in Queensland, south along the Great Divide Mountain Range to Tasmania and west to the Otway Range and the Grampians in Victoria, we conclude that several species likely occur under this name. In fact, Rothfels (1979: 522), in a cytological study of what might have been *A. aurantiaca* (as *Cnephia* A), reported the presence of two sibling species. Of particular note are the morphological difference between larvae of mainland *A. aurantiaca* (Fig. 36) and those from Tasmania (Fig. 37). The latter are distinct in colour, shape and size of the pupal gill histoblast, and size of the posterior proleg. The male paratypes designated by Tonnoir (1925) from Tasmania also exhibit differences from mainland material. It is highly likely that the Tasmania population of *A. aurantiaca* is specifically distinct from

those on the mainland. Another character state, the presence of small but distinct prothoracic proleg lappets in certain populations (Figs. 49–51) is perhaps also indicative of specific difference. This feature is markedly expressed in *A. strenua*, but is entirely absent from most populations of *A. aurantiaca*. The intermediate stage as expressed in certain populations of '*A. aurantiaca*' requires further scrutiny. Finally, the apically branched Rs, is distinct in some populations and less so in others (*i.e.*, is represented by just a few hairs in a row). Further morphological cytogenetic and molecular studies are needed to confidently circumscribe entities in this complex.

Males of *A. aurantiaca* and *A. strenua* are distinct, although the latter exhibits a great deal of colour variation (Tonnoir, 1925: 236). Overall the body in *A. aurantiaca* males is bright yellow (Fig. 18) whereas that of *A. strenua* is darker brown (Fig. 73). Further, the eyes of *A. strenua* males have fewer rows of larger upper ommatidia and are dark brown.

The ventral plate of *A. aurantiaca* is rather complex and must be interpreted with caution. Few of the males examined so far have the depressed apex of the ventral plate as illustrated by Mackerras & Mackerras (1950: their Fig 3), where it is described as being 'distinctly concave'. When examined in three dimensions, the tip is directed ventrally, giving the plate a concave appearance in ventral view (Fig. 25), thence the original description. If the ventral plate is flattened out on a slide mount (Fig. 27), it appears to be rounded apically. All males examined have parameres plate-like and broadly attached to both the gonocoxa and basal arms, with the paramere connection apparently absent. The parameres are tapered posteriorly with various development of small spines distally on the aedeagal membrane. Apical spines of the gonostylus are poorly developed in *A. strenua* (Mackerras & Mackerras, *loc. cit.*). Female *A. aurantiaca* possess a rugose-wrinkled spermatheca as originally described (Fig. 16). Pupa possess only a small pleurite on abdominal segment V (Fig. 35) and this agrees largely with Mackerras & Mackerras (1950: 169) who state that pleurites are absent.

Tonnoir (1925: 226. His Fig. 10B) illustrated the anal sclerite of *A. aurantiaca* larvae as having a distinct 'hole' at the posteromedial base of the structure and the posterolateral arms single, albeit substantial. With the widespread collections now available, the first character still is of value for identification, but the second not. The posteroventral arms are varied and while can be single, may be substantial and paralleled by a posterolateral arm, as seen in larvae of *A. strenua*. Similarly, as for *A. strenua* larvae, there are a large number of campaniform sensilla between the posterolateral arm, as there are number of hooks in the posterior circlet—indeed, these two character states are diagnostic for the *aurantiaca* species-group.

Mackerras & Mackerras (1955:105) noted that the Flinders Island (Bass Strait) population of *Austrocnephia aurantiaca* was subtly different from those of the mainland and Tasmania, but did not give any details. We illustrate (Fig. 46) the larval hypostoma, but with no recent material available we have not pursued their observation. However, with the gross differences in larvae (*cf.* Figs. 36, 37) of *A. aurantiaca* of the Australian mainland and Tasmania, as noted previously, we are fully of the opinion that they will be shown to be related but separate taxa.

Collection data reveals that *A. aurantiaca* was present in The Grampians National Park and environs from at least the mid 1950s through the mid 1990s; however, more recent efforts (2011, 2014) to collect this species from those same localities have proven unsuccessful. While high-velocity habitats remain within the Park, such as the Mackenzie Falls, the region has recently suffered from drought and intensive forest fires. Consequently, many of the watercourses where *A. aurantiaca* immatures were previously collected are now dry or characterized by low flow. Could an extended period of drought account for the apparent lack of *A. aurantiaca* from The Grampians? Other local species of simuliid, such as *Nothogreniera fergusonii* (Tonnoir) and *Simulium ornatipes* Skuse, are adapted to breed in intermittent streams that flow during the winter and early spring. Another commonly encountered species, *Austrosimulium furiosum*, is a generalist species that can breed in a wide variety of running water habitats. Whether *Austrocnephia aurantiaca* has truly been extirpated from The Grampians warrants further investigation.

The record (Fig. 196) of a single *A. aurantiaca* adult from Mt. Spec, Queensland, (clustered with *A. strenua*), should be regarded with caution. It is anomalously north of other known localities.

***Austrocnephia strenua* (Mackerras & Mackerras 1950). New combination.** (Figs. 58–98)

Cnephia strenua Mackerras & Mackerras 1950: 170; original description. Mackerras & Mackerras, 1955: 105.

Stegopterna (Z) *strenua*. Colbo, 1974: 67; unpublished reassignment.

Cnephia strenua. Rothfels, 1979: 522.

'*Cnephia* of authors' *strenua*. Crosskey, 1987: 443; Prosimuliini, undetermined genus.

strenua. Crosskey, 1989: 222; unplaced species of Prosimulini.

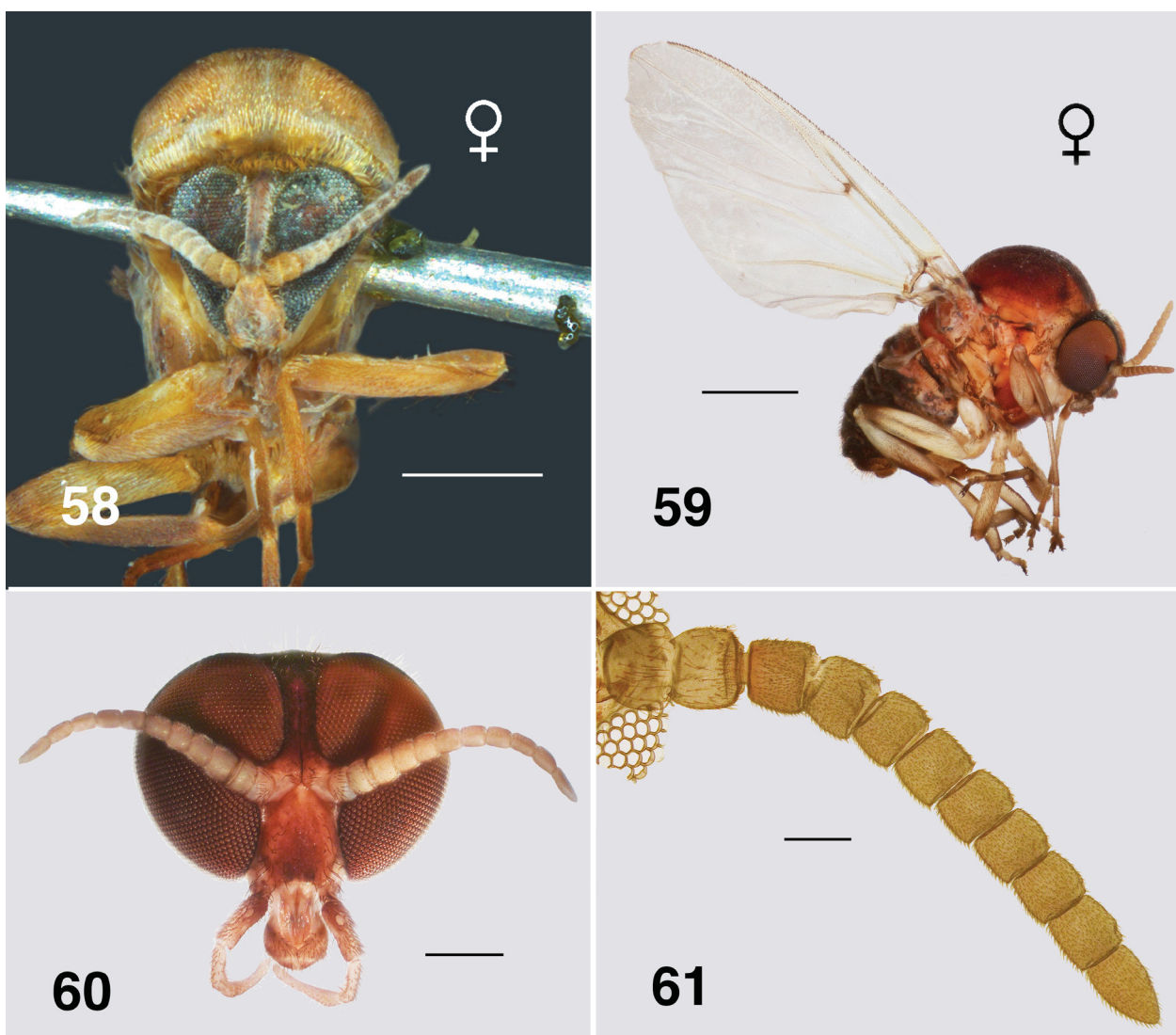
Paracnephia strenua. Crosskey & Howard, 1997: 18; Prosimuliini, new combination

'*Cnephia*' *strenua*. Moulton, 2000: 110. Moulton, 2003: 47.

Paracnephia strenua. Crosskey & Howard, 2004: 10; Prosimuliini, unplaced to subgenus.

Paracnephia strenua. Adler & Crosskey, 2008: 26, transferred to Simuliini. Adler, 2019:32; unplaced to subgenus.

Redescription. *Adult female* (based on large numbers of adults in alcohol). *Body* (Figs. 58, 59): head brown, thorax dark orange to dark yellow, abdomen overall black, yellowish anteriorly; total length 2.8–3.3 mm. *Head* (Fig. 60): width 0.97–1.00 mm; depth 0.70–0.73 mm; postocciput with dense yellow vestiture, frons narrow, parallel-sided, dark brown-black, vestiture of sparse hairs; frons:head width ratio 1.0:10.7; postocciput dark, vestiture of dense hairs. *Eyes*: interocular distance 0.09–0.11 mm; ommatidia diameter 0.025 mm; *ca.* 36 rows across and 48 down at mid-eye. *Clypeus*: width 0.25 mm; mottled in colour. *Antenna* (Fig. 61): elongate, extended well beyond posterior margin of head; total length 1.1–1.4 mm; scape and pedicel pale and similar in size to darker flagellomere I; flagellomeres II–VII, similar in size, brown, tapered finely to elongated apical flagellomere IX. *Mouthparts*: well developed, *ca.* 0.30–0.41× head depth; maxillary palp length 0.8–1.1 mm, palpomeres I & II markedly small, palpomere III darker brown than remainder, not densely hirsute, palpomere V twice as long as palpomere IV, proportional lengths of palpomeres III–V 1.0:0.6:1.3; sensory organ elongated, 0.5× length of palpomere III, opening large, 0.5× vesicle length; mandible (Fig. 62) of Souita Fall population is unique with *ca.* 14 outer teeth, 29–32 inner teeth, *ca.*



FIGURES 58–61. *Austrocnephia strenua* female. (58) Holotype, frontal view. (The Cascades, QLD). Image by LHG-A. Scale bar = 0.5 mm. (59) Habitus. (Souita Falls). Scale bar = 1.0 mm. (60) Head, frontal view. (Souita Falls). Scale bar = 0.25 mm. (61) Antenna. (Bartle Frere). Scale bar = 0.1 mm.

12 of those recurved and sharp, remainder angulate and blunt, other populations possess just a few outer teeth, most only inner teeth; lacinia with 19–21 outer and 9–13 inner teeth, smaller than in *aurantiaca*; cibarium (Fig. 63) with medial depression angulate and with apex convex, cornuae broad basally and markedly flared, slightly sculpted. *Thorax*: length 1.7–2.0 mm; width 1.3–1.7 mm; overall dark yellowish orange, with distinct dorsocentral vittae of golden scales and pale lateral lines; postpronotal lobe well developed with vestiture similar to scutum—even sparse fine small hairs; scutellum markedly paler than scutum, vestiture of sparse very fine yellowish hairs centrally, distinct longer black hairs laterally; postnotum concolourous with scutellum, vestiture similar; anteprenotal lobe with sparse yellow hairs; proepisternum and fore coxa with sparse hairs; anepisternal membrane yellowish brown, bare; katepisternum dark brown, as long as deep, sulcus shallow and broad. *Wing* (Fig. 64): length 4.2 mm; width 2.0 mm; membrane occasionally very slightly fumose on apex and anal lobe, with lightly pigmented spot at junction of r-m cross vein and R_1 ; distal 2/3 of costa with mixture of hairs and spines, R_s narrowly divided distally (R_{2+3} in some specimens expressed as simple row of hairs); area between Sc and R light yellow; a:b ratio 1.0:2.5; basal medial cell minute or absent; M_1 typically appearing doubled, sometimes tripled; CuA not markedly sinuous; CuP extended to wing margin in some specimens; A_1 not reaching margin. *Haltere*: stem clear, knob dark tan. *Legs*: coxae and femora mostly yellowish, the latter dark brown apically; tibiae with basal quarter yellowish, remainder dark; hind basitarsus with ventral row of sparse stout spines; calcipala markedly longer than wide (Fig. 65); pedisulcus not markedly developed—at most represented by wrinkled cuticle; tarsomere II 2.5–3.1× longer than apical width; claw (Fig. 66), with main talon strongly curved and evenly tapered, slightly serrated along inner edge, basal tooth 0.3× length of claw, heel rounded. *Abdomen*: basal scale medium brown, vestiture of long dense hairs; anterior few segments yellowish, remaining posterior segments mottled blackish brown; tergite II weakly sclerotized and V-shaped, tergites III & IV rectangular, broader in more posterior segments; vestiture markedly expressed in segments III and further back. *Genitalia*: markedly small; sternite VIII with distinct microtrichial array medially, larger stronger hairs posterolaterally; hypogynial valves (Fig. 67), lightly pigmented, vestiture of triads of microtrichia and strong hairs, medial edges of valves slightly convex but not touching, anteromedial edges slightly strengthened; narrowly rounded apically with poorly defined edges, medially with raised area; genital fork (Fig. 68) with anterior stem relatively long and narrowed, deflected slightly ventrally, slightly expanded apically, indication of membranous lateral area in stained specimens, posterolateral arms narrow, lateral plate trapezoid or diamond-shaped, without anteriorly directed apodeme; spermatheca ovoid (Fig. 70), elongated, dark brown, lightly tuberculate, internal fine spines (acanthae) absent, with small rounded membranous area at junction with spermathecal duct; cercus (Fig. 69) in lateral view bluntly cone-shaped, slightly constricted medially; anal lobe subequal in size to cercus, both with vestiture of long hairs and dense microtrichia. *Egg*: sub-triangular in lateral view (Fig. 71), *ca.* 0.19 by 0.11 mm, with *ca.* 600 counted in a single dissected female from Lamington National Park, Queensland.



FIGURES 62, 63. *Austrocnephia strenua* female. (62) Mandible apex. (Souita Falls). Scale bar = 0.05 mm. (63) Cibarium. (Souita Falls). Scale bar = 0.1 mm

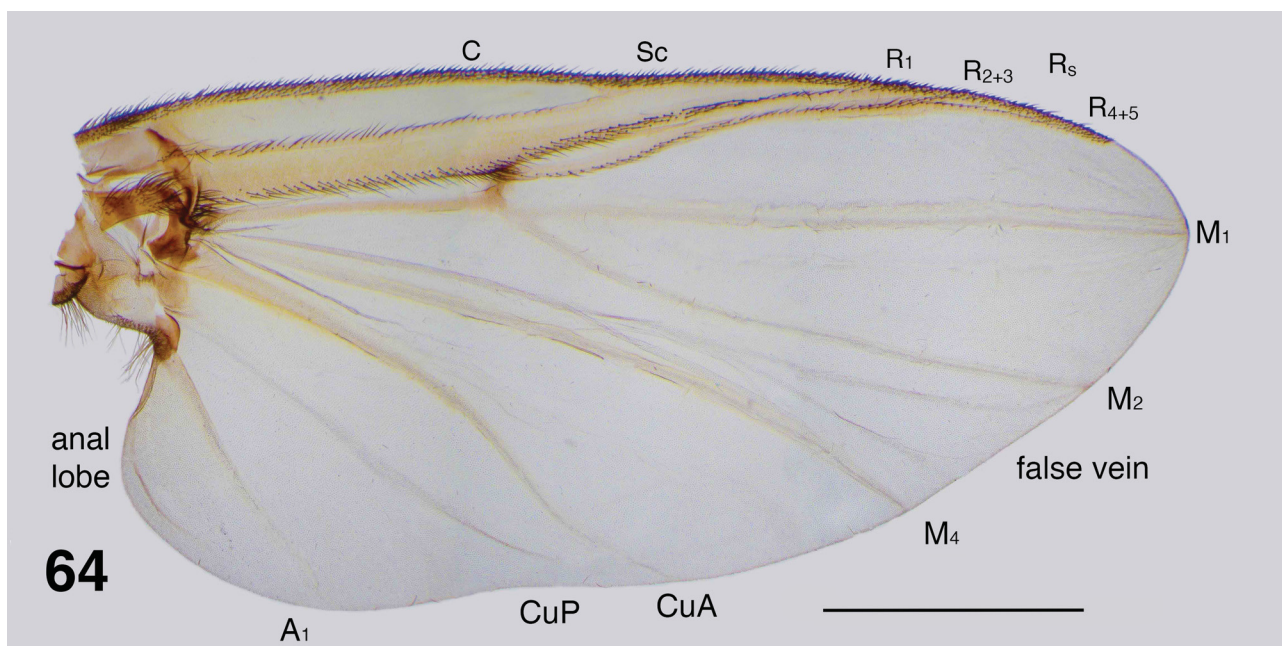
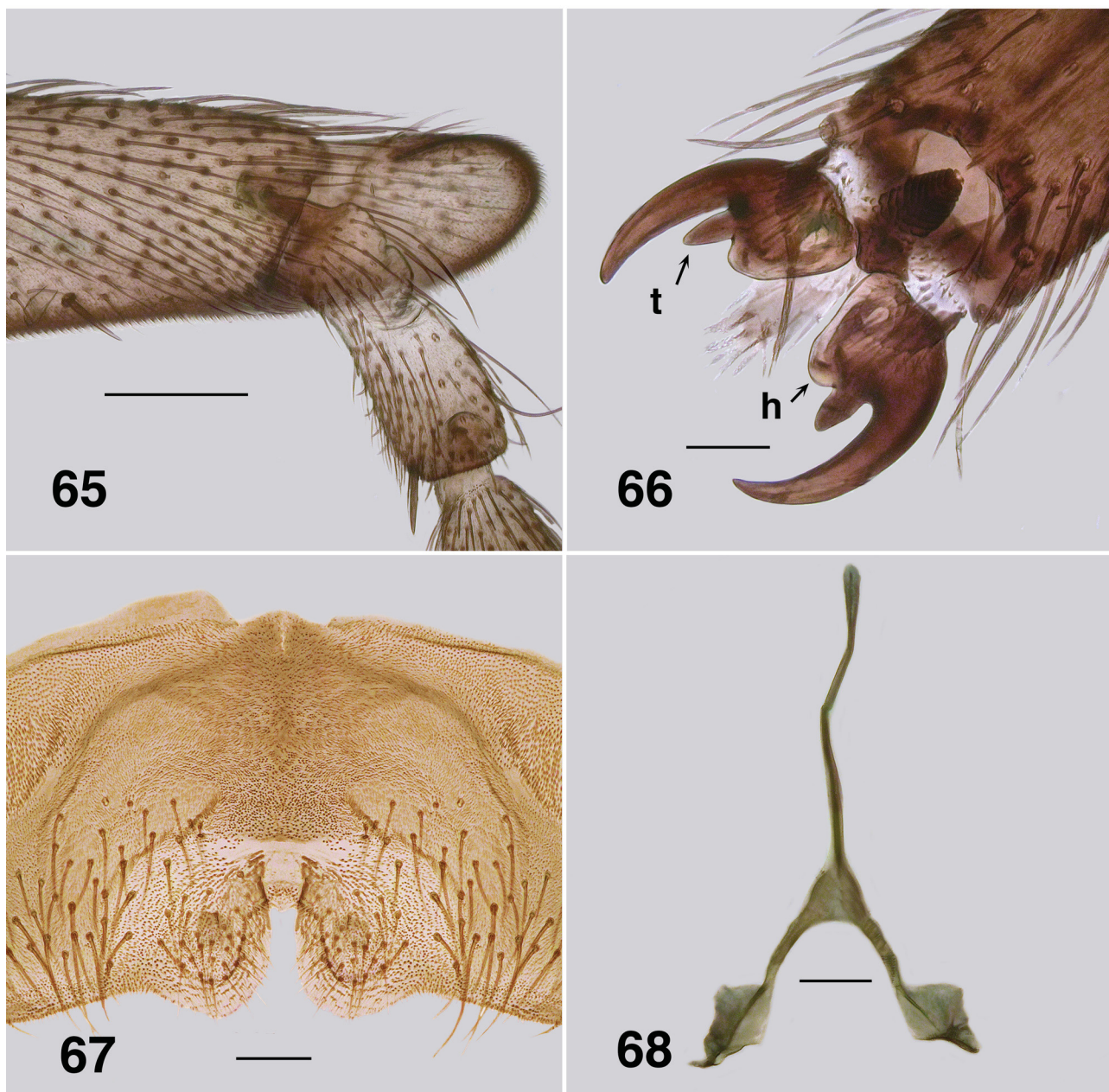


FIGURE 64. *Austrocnephia strenua* female. (64) Wing. (Souita Falls). Scale bar = 1.0 mm.

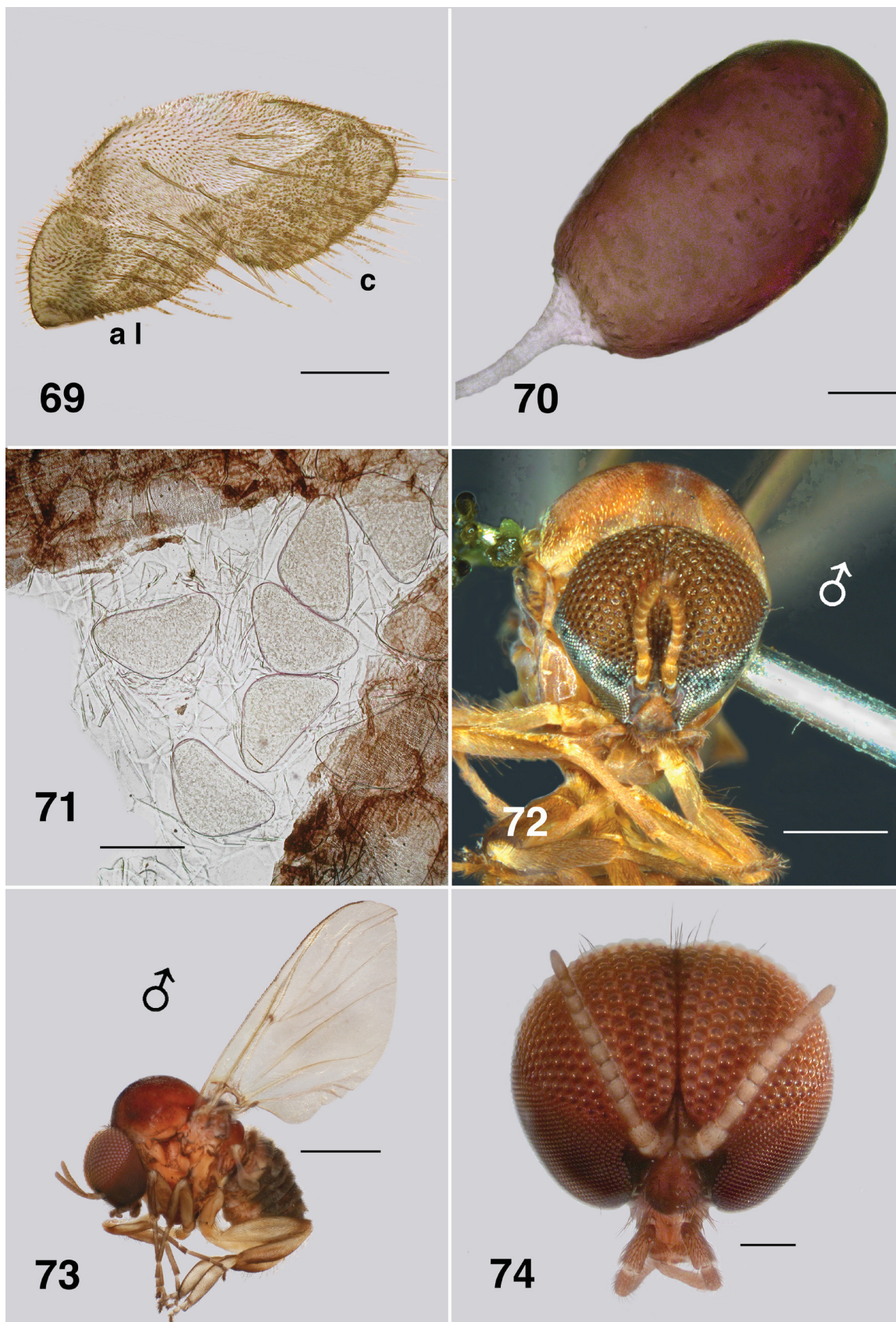
Adult male (numerous specimens). *Body*: pinned specimens light brownish orange (Fig. 72), dark brownish orange and black in ethanol preserved specimens (Fig. 73); total length 3.3–3.5 mm. *Head* (Fig. 74): width 1.0–1.2 mm; depth 0.87–1.0 mm. *Eyes*: upper ommatidia dark brown, enlarged, diameter 0.076 mm, *ca.* 13–16 across and down; lower ommatidia black to blackish orange/brown, markedly smaller, diameter 0.027 mm, 34–36 across and down. *Clypeus*: blackish brown; width 0.19–0.27 mm; vestiture of sparse fine black hairs. *Antenna* (Fig. 75): markedly elongated, total length 0.76–1.0 mm; pedicel and scape darker; scape and pedicel subequal in size, flagellomere I narrower than scape and twice as long as wide, pale basally, flagellomeres less tapered than those in *A. aurantiaca*, overall light brown. *Mouthparts*: insubstantial; length 0.14–0.20× head depth; maxillary palp, essentially as for *A. aurantiaca*, 0.55–0.92 mm long, palpomeres I & II small, palpomere III shorter than palpomere IV, palpomere V elongated, proportional lengths of palpomeres III–V 1.0:0.6:1.6, sensory vesicle small, occupying 0.33× palpomere width, opening 0.5× vesicle width; lacinia small, lacking teeth, but with apical hairs; mandible weakly developed and lacking teeth. *Thorax*: markedly domed, head angled anteriorly; length 1.6 mm; width 1.3 mm; postpronotal lobe with longish fine pale hairs, concolourous with scutum; anteppronotal lobe with distinct patch of fine pale hairs, proepisternum bare; scutum evenly yellow, vestiture of evenly sparse short fine pale hairs, dense and long in scutellar depression; scutellum lighter than scutum, with markedly elongate yellow and black hairs; pleuron brown, anepisternal membrane bare, katepisternum dark brown, sulcus distinct, but shallow; metathoracic furcasternum lacking flared anterior flanges. *Wing*: length 3.6–3.9 mm, width 1.9–2.0 mm; a:b ratio 1.0:2.6; otherwise as for female. *Haltere*: stem pale, knob tan. *Legs*: overall yellowish, lighter than female; calcipala markedly longer than wide; pedisulcus poorly developed, at most represented by wrinkled cuticle; tarsal claw with truncated basal tooth and grappling hook of 23–26 teeth. *Abdomen*: black dorsally and posteriorly, pale anteroventrally, basal scale black, hairs black, extended to posterior of segment IV on contracted abdomen, tergites poorly sclerotized, tergite II 2.5× as wide as long, pigmented only medially, tergite III, narrower, but pigmented laterally, other tergites broader, increasingly so posteriorly and less fully pigmented, vestiture of sparse long hairs, more so posteriorly; sternites moderately developed and hirsute, more so posteriorly. *Genitalia*: small, not heavily pigmented (Fig. 76); cerci well developed; gonocoxa 1.3× longer than basal width, posteromedially strengthened and slightly fluted, margin extended beyond articulation with gonostylus, hirsute with long black sparse hairs and microtrichia; gonostylus in ventral view narrowed, approximately 1.8× longer than basal width, with two substantial apical spines (Fig. 77); ventral plate small, 1.7× wider than long in ventral view with variably-shaped posterior lip; Souita Falls population (Fig. 76) with lip short, narrowed at base and with broadly rounded apex; Behana Gorge population (Fig. 78) with lip long, not narrowed at based, and with apex narrowly rounded; basal arms elongated; paramere connector short and broad; median sclerite with two short variably expressed sclerotized arms projected dorsally (Fig. 79); paramere

in all populations triangular, plate-like basally, slightly strengthened along ventral edge, tapered distally with irregular ridges; adeagal membrane either bare or with a few, short, weakly expressed spinules near apex of paramere.

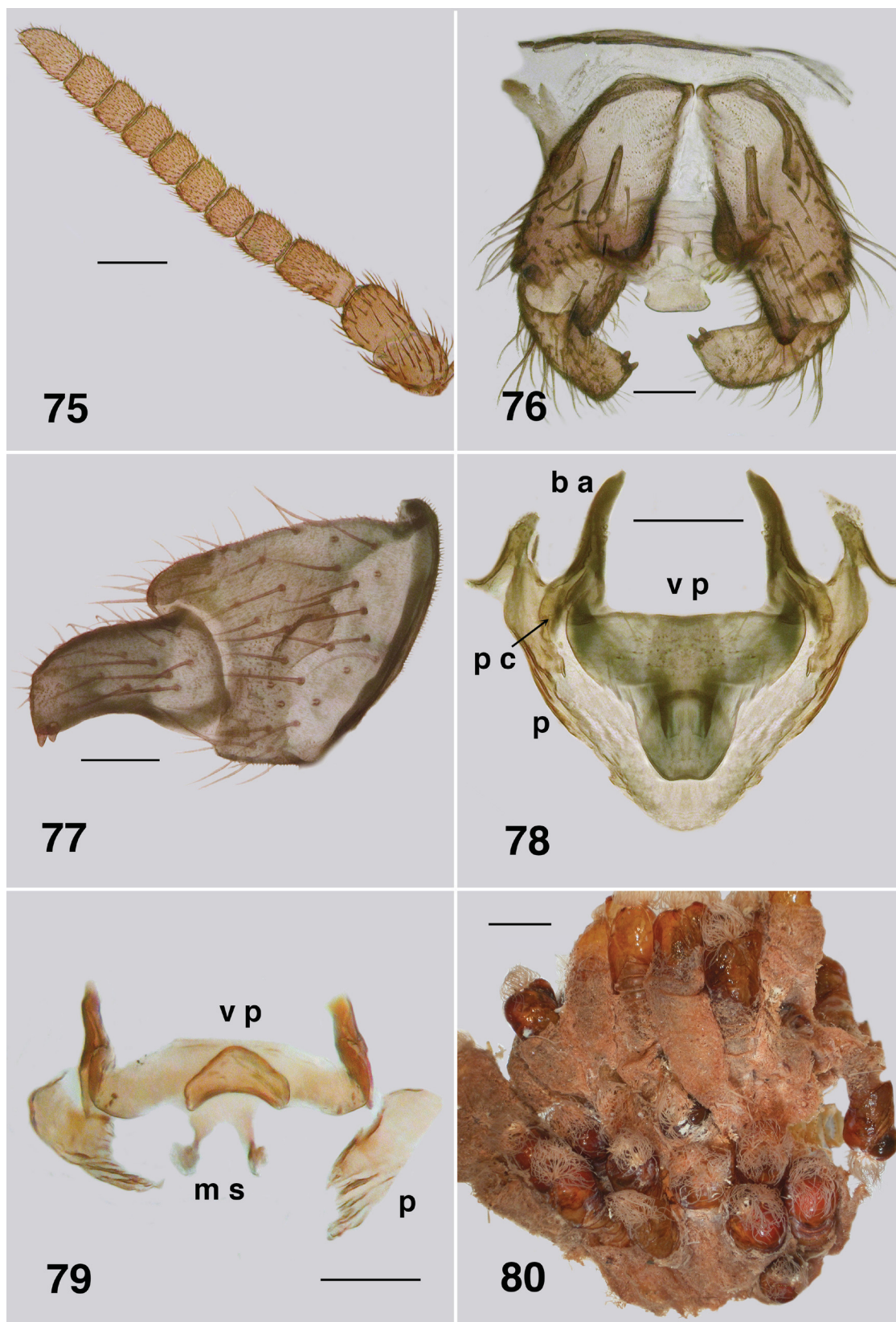


FIGURES 65–68. *Austrocnephia strenua* female. (65) Calcipala and pedisulcus. (Souita Falls). Scale bar = 0.1 mm. (66) Tarsal claws showing basal tooth (t) and heel (h). (Souita Falls). Scale bar = 0.02 mm. (67) Hypogynial valves. (Bartle Frere). Scale bar = 0.05 mm. (68) Genital fork. (Bartle Frere). Scale bar = 0.05 mm.

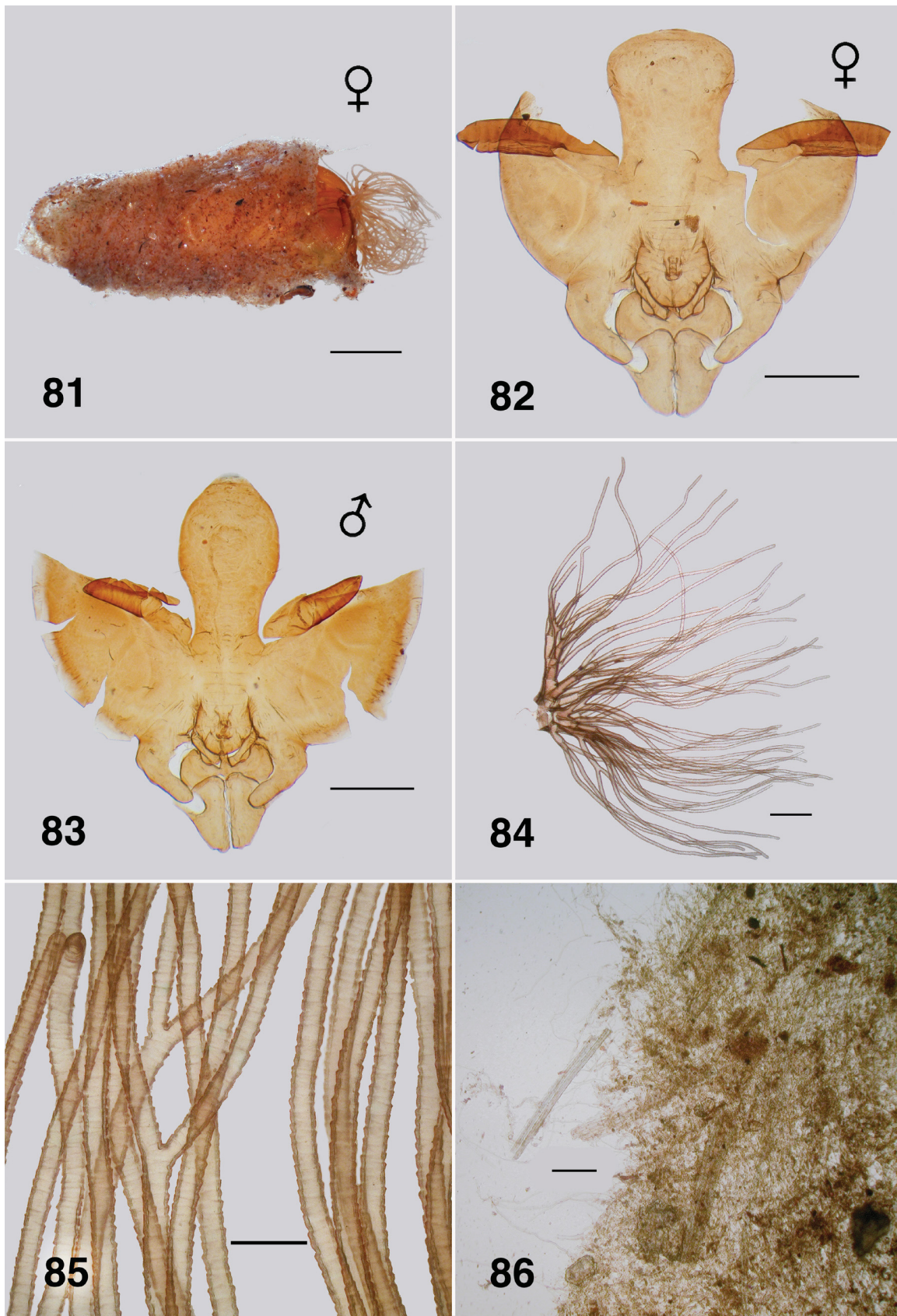
Pupa (numerous specimens, Bartle Frere & Souita Falls). Typically found clumped in large masses (Fig. 80). *Body*: female length 4.8–5.0 mm (Fig. 81), male length 4.5–4.7 mm; brown and yellow, markedly sclerotized with strong cuticle, with or without tubercles. *Head*: frons of female (Fig. 82) broad and apically truncated, with ratios of basal width to vertex width and height 1.0:1.2 and 1.0:1.7 respectively; frons of male (Fig. 83) narrow and apically tapered, ratios 1.0:1.8 and 1.0:2.8 respectively; cuticle lightly sculpted but lacking tubercles; dorsolateral frontal setae and facial setae present in males; three sensilla typically present in females, all closely grouped on ocular sclerite beside/beneath antennal sheath, rarely with one on dorsal frons; all setae substantial, without curled tips; antennal sheath of female extended beyond margin of ocular shield, that of male not so extended. *Thorax*: markedly domed, slightly less so than in *A. aurantiaca*, smooth, with dorsal trichoid setae short, curved but not curled at tip. *Gill* (Fig. 84): total length 1.2–1.5 mm, with 48–55 light brown filaments arising from 5 or 6 short pale trunks; filaments not



FIGURES 69–71. *Austrocnechia strenua* female. (69) Cercus (c) and anal lobe (a l). (Bartle Frere). Scale bar = 0.05 mm. (70) Spermatheca. (Souita Falls). Scale bar = 0.05 mm. (71) Eggs. (Lamington Nat. Park). Scale bar = 0.2 mm. **FIGURES 72–74.** *Austrocnechia strenua* male. (72) Paratype. (The Cascades). Image by LHG-A. Scale bar = 0.5 mm. (73) Habitus. (Souita Falls). Scale bar = 1.0 mm. (74) Head, frontal view. (Souita Falls). Scale bar = 0.2 mm.



FIGURES 75–79. *Austrocnephia strenua* male. (75) Antenna. (Behana Gorge). Scale bar = 0.1 mm. (76) Genitalia, ventral view. (Souita Falls). Scale bar = 0.05 mm. (77) Gonocoxa and gonostylus. (Behana Gorge). Scale bar = 0.05 mm. (78) Slide mounted genitalia showing basal arms (b a), parameres (p), paramere connector (p c), ventral plate (v p). (Behana Gorge). Scale bar = 0.05 mm. (79) Apical view of genitalia showing median sclerite (m s), parameres (p) and ventral plate (v p). (Souita Falls). Scale bar = 0.05 mm. **FIGURE 80.** *Austrocnephia strenua* pupae. (80) Pupal mass. (Souita Falls). Scale bar = 2.0 mm.



FIGURES 81–86. *Austrocnechia strenua* pupa. (81) Female pupa. (Souita Falls). Scale bar = 1.0 mm. (82) Female cephalic capsule. (Souita Falls). Scale bar = 0.5 mm. (83) Male cephalic capsule. (Souita Falls). Scale bar = 0.5 mm. (84) Pupal gill. (Behana Gorge). Scale bar = 0.2 mm. (85) Gill filament surface. (Souita Falls). Scale bar = 0.05 mm. (86) Cocoon silk. Scale bar = 0.2 mm.

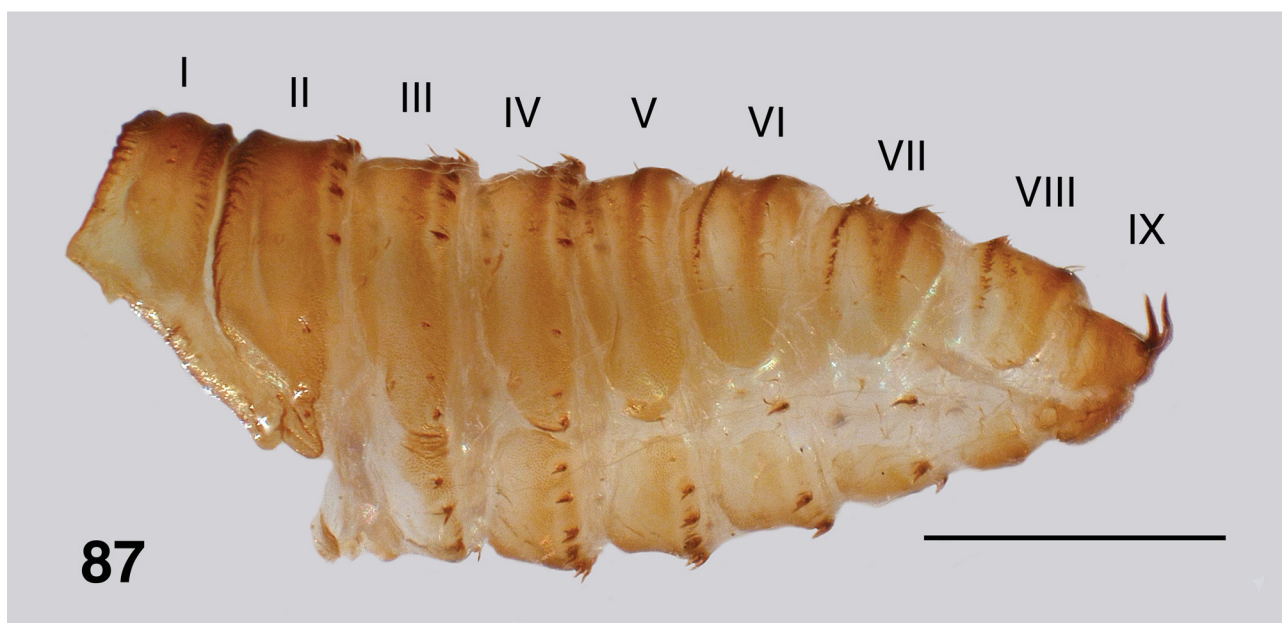


FIGURE 87. *Austrocnephia strenua* pupa. (87) Abdominal armature. (Bartle Frere). Scale bar = 1.0 mm.

markedly tapered, bifurcated at irregular distances from base, ventral filaments directed anteriorly, dorsal filaments directed dorsally, with one or two longer filaments reflexed posteriorly over the thorax; filament surface pseudoannulated throughout (Fig. 85). *Abdomen* (Fig. 87): well sclerotized, especially the anterior tergites; tergites III & IV extended more ventrad than other tergites, separated from sternite by narrow band of striate membrane; segment V with small pleurite present, fused to tergite; other pleurites absent, replaced with minute plates underlying lateral hooks on segments VI & VII; abdomen with minute rounded tubercles, present or occasionally absent—when present sparser on terminal segments. Abdominal armature well developed; tergite I with fine hairs; tergites II–IV each with 4+4 central and 3+3 lateral anteriorly directed long thin recurved hooks (similar to the ventral hooks), lateral smaller than central; tergite V with four hairs and poorly expressed spine comb; tergites VI & VII with well developed spine comb anteriorly and posterior double pair of fine hairs on each side; tergite VIII with small spine comb and a pair of fine hairs posteriorly on each side; segment IX with sharply tapered slightly curved terminal spines, numerous other simple, long curved terminal setae; sternite III with 3+3 anteriorly directed simple recurved hooks, sternite IV with 5+5, sternite V with 5+5, sternite VI with 2+2, and sternite VII with 1+1; pleurites VI & VII with 1+1 anteriorly directed simple recurved hooks.

Cocoon: Length 3.0–4.0 mm, close fitting, often covering whole pupa, or just to half of the thorax, gills extended; irregular weave, less unorganized than others in the genus, silk fibers (Fig. 86) light brown and thick, some markedly so and strong; extraneous material from substrate incorporated.

Larva (based on numerous last instar larvae). *Body* (Fig. 88): total length 8.0–11.0 mm, evenly mottled brown, smoothly expanded from the head posteriorly, expanded posteroventrally. *Head* (Fig. 89): relative to body, small, evenly dark brown; head spot pattern poorly developed, but positive; length 0.80–1.15 mm, width 0.73–0.93 mm; distance between antennal bases 0.43–0.55 mm; anterior margins of head tapered anteriorly, straight, broadest posterior to stemmata; ecdysial lines markedly visible, divergent albeit straight until posterior of stemmata, then broadly curved medially; cervical sclerites distinct and finely joined to postocciput, varied; genae markedly dark brown. *Antenna*: short, not extended to end of labral fan stem; total length 0.30 mm; basal article short and clear proximally, dark brown distally, medial article and distal articles dark brown with marked clear junction, subequal in length; two sensilla at junction markedly pointed; basal article shorter than medial article, proportional lengths of basal, medial, and apical articles 1.0:1.4:1.5; medial article expanded towards distal junction, distal article longer than in *A. aurantiacum*. *Labral fan*: stem short and dark brown, *ca.* 43–50 fine rays, six to ten posterior rays finer than remainder, length *ca.* 0.66 mm, mid-ray width 0.015 mm; pattern of microtrichia not markedly developed, larger microtrichia longer than ray width, four or five smaller microtrichia interspersed, varied. *Mandible* (Fig. 90): darkly pigmented; short; brushes markedly developed; dorsal margin slightly more curved than in *A. aurantiaca*; outer, apical and subapical teeth not accentuated, subequal in length; six to seven spinous teeth, distal two teeth markedly

developed (but varied); serration small, often no evidence of sensillum; blade region smoothly convex. *Maxilla*: palp cone-shaped 1.8–2.0× as long as basal width, darkly pigmented; dense tuft of hair and long spinous hairs at base of palp. *Postgenal cleft* (Fig. 91): moderately developed, shallow, U-shaped, sclerotized with slightly irregular edges and occasionally a small medial projection; posterior tentorial pits small and rectangular in shape; postgenal bridge evenly lighter brown; elongated posteroventral muscles spots not markedly obvious; ratio of hypostoma: genal bridge: postgenal cleft variable—1.0:1.5(1.7):0.5(0.8). *Hypostoma* (Figs. 92, 93): small, darkly pigmented and not markedly extended from head margin, lateral margins gently sloped; teeth in various arrangements; tooth 0 prominent, flanked by teeth 1–3, subequal, 2 & 3 sometime smaller and varied; tooth 4 slightly larger than previous teeth, slightly flanged basally, teeth 5–7 markedly small and difficult to observe, tooth 8 often directed laterally; lateral serrations on hypostoma absent; six to eight substantial, closely-packed hypostomal setae on each side; ventral edge of hypostoma not markedly developed, still, slightly obscuring teeth 5–7. *Thorax* (Fig. 94): anteriorly mottled brown, remainder pale; pupal gill histoblast with 5–7 basal trunks visible, broadly L-shaped, directed ventrally, then sharply posteriorly, broadly rounded with filaments directed anteriorly then dorsally, some bifurcations visible. *Prothoracic proleg*: strongly developed with distinct L-shaped lateral plates; lateral lappet extensions markedly obvious (Fig. 95), in some localities shorter and broader, or apparently not extended. *Abdomen*: evenly mottled brown; expanded evenly posteriorly. *Ventral tubercles*: absent. *Anal sclerite* (Fig. 96, 97): complex and variable, anterolateral arms basically just anterior flanges of the medial region, itself various; medial region with the well developed posteromedial space sometimes closed off to form a hole, posterolateral arms from medial region parallel the elongated, substantial posteroventral arms—giving appearance of doubled ventral arms (also in earlier instars); elongated extensions from the medial ends of the posteroventral arms between the dorsal junction of circlet of hooks variable—not well developed. Array (14 or 15) of campaniform (sometimes as markedly short setae) sensilla between the posteroventral arms and circlet of hooks, varied. *Rectal papillae*: three simple lobes. *Posterior circlet*: markedly developed and directed slightly ventrally on posterior abdomen; large numbers of hooks, *ca.* 340 rows of hooks with *ca.* 50 hooks per row (total *ca.* 17,000).

Etymology. Named by Mackerras & Mackerras (1950: 172), literally, for the preferred strenuous habitat of larvae—that of high velocity water.

Types. The type locality is Queensland, Cairns, Cascades, Freshwater Creek (S16.9300° E145.6900°). Adult. Coll. Mackerras. ANIC. The female holotype and two male paratypes were examined by LHG-A in 2007. Exact labeling not recorded.

Additional material examined: Two pinned specimens from ANIC were examined by DAC in detail. One, a female from [Little Crystal Cr./ Mt Spec, N.Q./ 6.12.54] [bred out] [C. strenua/ det. J. Prince] [Aust. Nat. Ins. Coll.], the other a gravid female from [Lamington/ Nat. Pk., Qld/ 6-1-.ii.1961/ I. C. Yeo] [Gressitt/ Trap] [Open forest] [Cnephia nr/ strenua/ det. J. Prince] [Aust. Nat. Ins. Coll.]. Both specimens are now slide mounts in ANIC.

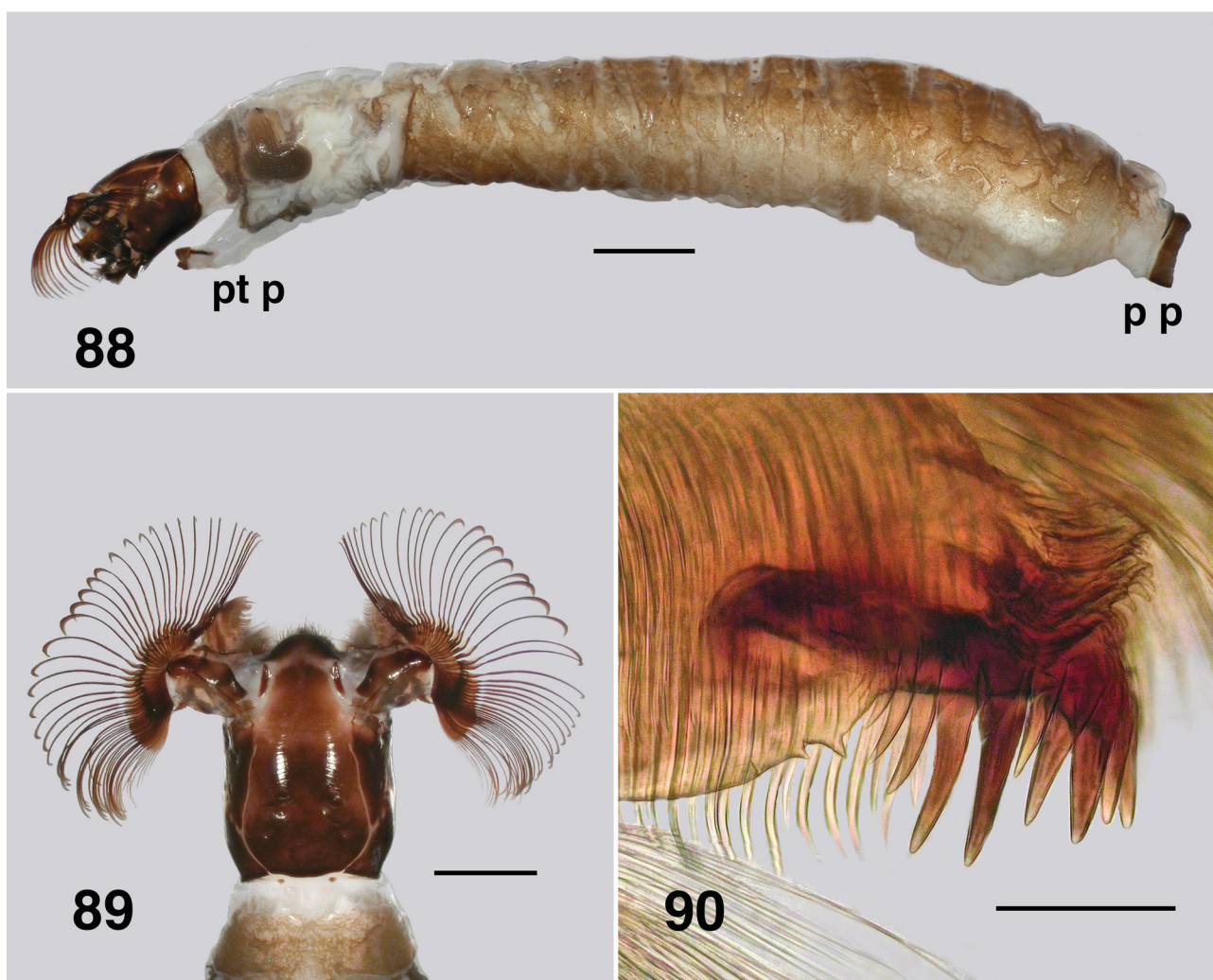
Alcohol material: Large numbers of larvae and pupae from collections by P. & H. Zwick, made mainly in the 1970's. [ANIC Database No. 29 026508–523, 29 026525–528, 29 026530–531]. Also, considerable material of all stages collected, in the main, by JKM, 1996. [UASM#/370803–370806, 370827, 370828]. **Slide mounts:** All stages [UASM#/370749–370781].

Bionomics. Both Mackerras & Mackerras (1950:170) and Colbo (1974) noted that little was known about this species. It appears, however, to be multivoltine since later instar larvae plus pupae have been found from October to June—an Austral early summer to autumn species. Colbo (1974), though, noted that for SE Queensland the season was April to November—an extended 'winter' species? For Northern Queensland the season was from September to December, a 'spring' species. There is no useful information on water temperatures.

There is no record of this species biting humans and no adults have been taken in the field. For the Souita Falls population, however, females possess teeth on both sides of the mandible (unique in the genus), have poorly developed abdominal tergites, maxillary palp sensory vesicle well expressed and a substantial tarsal claw basal tooth, characters that point to probable ornithophily (Shewell, 1955; Sasaki *et al.*, 1985; Adler *et al.*, 2004).

The number of eggs from the gravid Lamington specimen, *ca.* 600, is towards the upper numbers of eggs known for simuliids (Crosskey, 1990: 462) and again, suggests blood feeding rather than autogeny.

Larvae and pupae are often clumped, with the latter forming mats of overlapping specimens, most of similar developmental stage. That aspect of the biology is discussed later. Mackerras & Mackerras (1950: 173) noted that larvae are found in extremely fast flow to the point where they are difficult to collect. Pupae were in lower velocity. Recent collections are in full agreement.



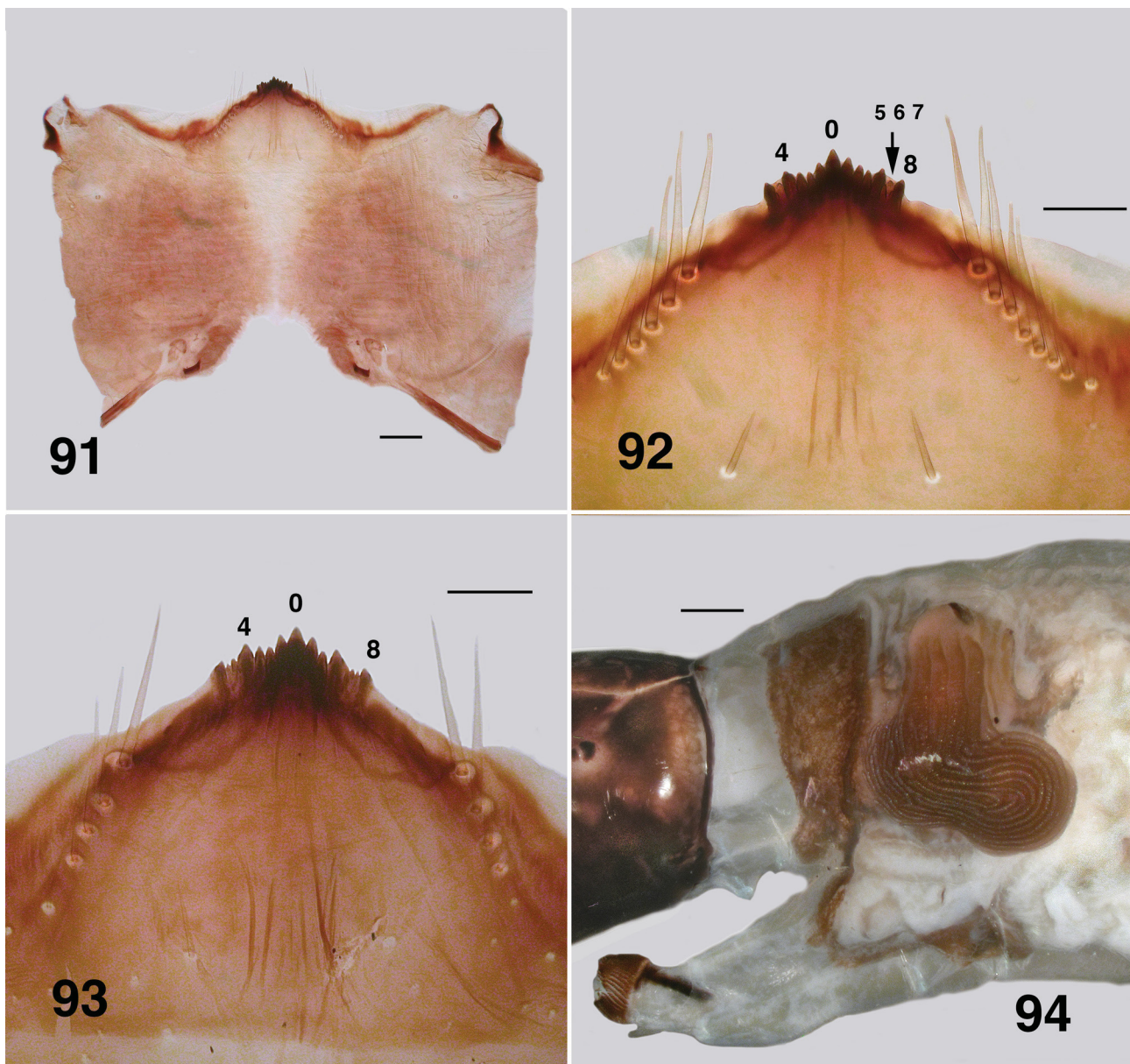
FIGURES 88–90. *Austrocnephia strenua* larva. (88) Habitus, last instar, showing prothoracic (pt p) and posterior prolegs (p p). (Souita Falls). Scale bar = 1.0 mm. (89) Head, dorsal view, last instar. (Souita Falls). Scale bar = 0.5 mm. (90) Mandible apex. (Behana Gorge). Scale bar = 0.05 mm.

Distribution (Fig. 196). *Austrocnephia strenua* is the most northerly-distributed member of the genus.

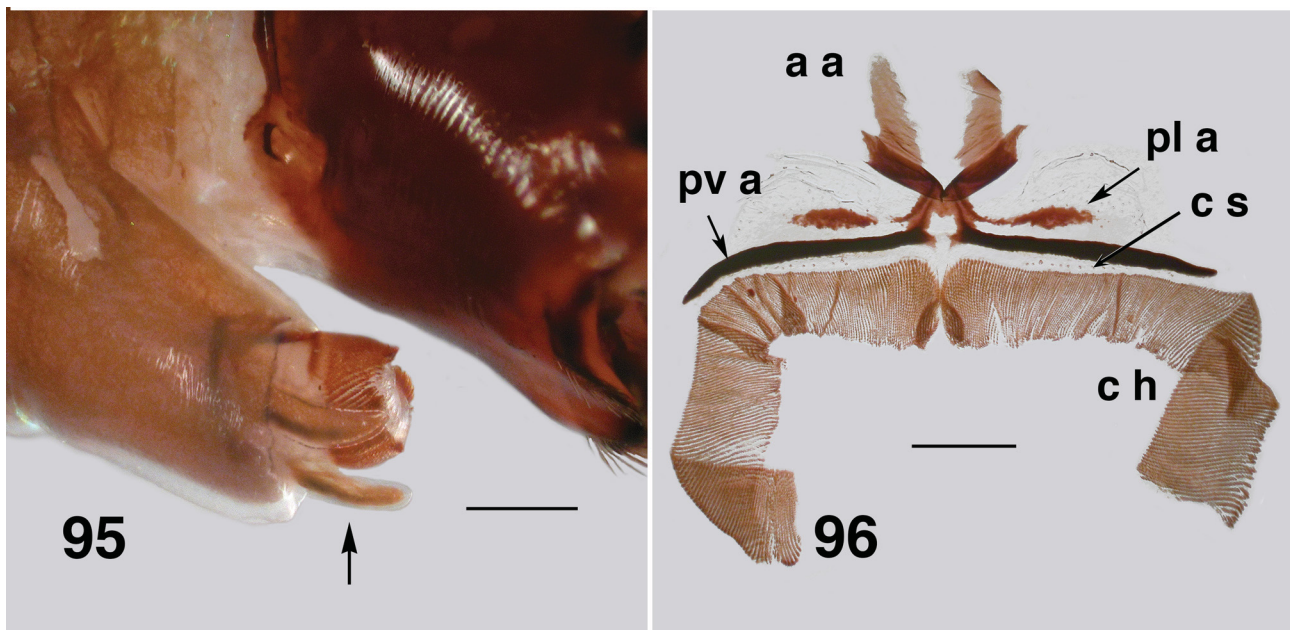
Queensland: Mossman, Mossman Gorge, S16.4748° E145.3432°. 18 Oct. 2002, Larvae, pupae. Coll. Zwick (ANIC). Mossman Gorge, near Cairns, S16.4748° E145.3432°. 20 Feb. 1973. Larvae, pupae. Coll. Zwick (ANIC). Mossman Gorge, Rex Creek, main stream, S16.4695° E145.3291°. 26 Mar. 1992. Larvae. Coll. H. & P. Zwick (ANIC). Mossman Gorge, S16.4748° E145.3432°. Coll. Cantrell (Colbo 1974). Redlynch, nr. Cairns, Crystal Cascade, tributary, S16.9617° E145.6794°. 5 Apr. 1997, Larvae, pupae. Coll. Zwick (ANIC). Freshwater Creek, nr. Cairns, S16.9617° E145.6794°. 5 Jan. 1973, Larvae. Coll. B. Cheesman (ANIC). Cairns, Freshwater Creek, S16.9617° E145.6794°. 15 Sept. 1949. Larvae. Coll. Mackerras (UASM, ANIC). Malandra, The Crater, S17.2800° E145.6200°. 27 Jun. 1971. Larvae. Coll. E. Riek (ANIC). Ringrose National Park, Atherton, S17.4200° E145.4800°. Coll. Cantrelli (Colbo 1974). Malandra, upper Barron R., Dinner Falls, S17.4331 E145.4833°. 24 Oct. 2002. Larvae. Coll. Zwick (ANIC). Mt. Bartle Frere, Josephine Falls, S17.4420° E145.8600°. 6 April 1997. 10 Dec. 1997. Larvae, pupae. Coll. Zwick (ANIC). Souita Falls, nr. Millaa Millaa, S17.5600° E145.6500°. 6 Mar. 2001. Larvae, pupae. Coll. H. & P. Zwick (ANIC). Atherton Tablelands, Souita Falls, Middlebrook Rd., ex. Old Palmerston Rd, S17.5600° E145.6500°. 18 Oct. 1996. Larvae, pupae, adults. Coll. J. K. Moulton (UASM). Atherton Tablelands, nr. Millaa Millaa, S17.5000° E145.600°. 19 Oct. 2002. Larvae, pupae. Coll. Zwick (ANIC). Palmerston Hwy., nr. McHugh Bridge, Little Beatrice River, S17.5521° E145.6092°. 22 Feb. 1973. Larvae. Coll. Unknown (ANIC). Atherton Tablelands, Emerald Ck., S17.0580° E145.5470°. 1 Jan. 1998. Larvae. Coll. A. Zwick (ANIC). Fishery Falls, S17.1800° E145.8800°. 29 Jun. 1971. Coll. E. Riek (ANIC). South of Gordonvale, Behana Gorge, Clamshell

Falls, S17.1894° E145.8233°. 28 Mar. 1997. Larvae. Coll. Zwick (ANIC). Behana Gorge, nr Cairns, S17.1650° E145.8320°. 12 Feb. 1973. Larvae. Coll. Zwick. 29 Jun. 1971. Pupae. Coll. E. Riek (ANIC). Mt. Bartle Frere, Josephine Falls, S17.4328° E145.8597°. 10 Oct. 1997. Larvae, pupae. Coll. A. Zwick; 24 Mar. 1992. Coll. H. & P. Zwick (ANIC). Little Crystal Creek, 45 m N of Townsville, S18.979° E146.197°. (November–December) Mackerras & Mackerras (1950). Paluma Range, Mt. Spec Road, Little Crystal Creek, S19.0154° E146.2656° (Bugledich 1999); 19 Mar. 1997, Larvae. Coll. Zwick. 12 Apr. 2002, Coll. A. Zwick (ANIC). Springbrook National Park, Purling Brook Falls, S28.1898° E153.2709° (Colbo 1974). Lamington National Park, S28.2200° E153.1500°. Bugledich (1999: 328). Lamington Plateau, Elabana Falls, S28.2500° E153.1497°. 26 December 1954. Coll. Mackerras (ANIC). Wilsons Peak, Teviot Brook, S28.2500° E152.4800°. 23 Apr. 1971. Larva, pupa. Coll. M.H. Colbo (ROM) Springbrook, Wilsons Peak, Condamine River, near Queen Mary Falls, S28.3400° E152.3735°. April–November. (Colbo 1974). Lamington Nat. Park, Binna Burra, Lower Ballanjui Falls, S28.2166° E153.2333°. 9 Mar. 1997. Larvae, pupae. Coll. Zwick (ANIC). Wilsons Peak, Teviot Brook, S28.2500° E152.4800°. 23 April 1971. Larvae, pupa. Coll. Zwick (ANIC).

New South Wales: Blue Mountains National Park, Bridal Veil Falls, Govetts Leap, S33.6333° E150.3129°. 5 Nov. 18 1998; Oct. 2014. Larvae, pupae. Coll. D.A. & R.E.G. Craig (UASM).



FIGURES 91–94. *Austrocnephia strenua* larva. (91) Ventral head cuticle. (Behana Gorge). Scale bar = 0.1 mm. (92) Hypostoma. (Behana Gorge). Scale bar = 0.05 mm. (93) Hypostoma. (Govetts Leap). Scale bar = 0.05 mm. (94) Pupal gill histoblast. (Souita Falls). Scale bar = 0.2 mm.



FIGURES 95, 96. *Austrocnephia strenua* larva. (95) Prothoracic proleg—arrow indicates lappets. (Mossman Gorge). Scale bar = 0.2 mm. (96) Anal sclerite showing anterior arms (a a), campaniform sensilla (c s), posterolateral arms (pl a), posteroventral arms (pv a), and circlet of hooks (c h). (Bartle Frere). Scale bar = 0.2 mm.

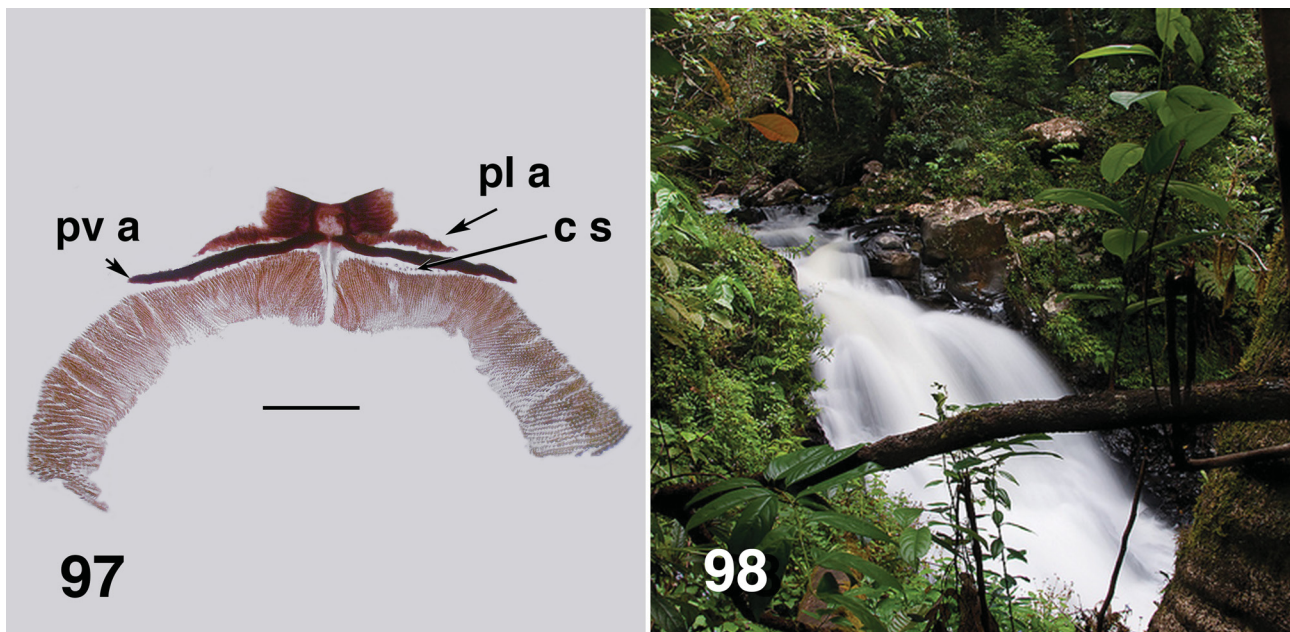


FIGURE 97. *Austrocnephia strenua* larva. (97) Anal sclerite showing campaniform sensilla (c s), posterolateral arms (pl a), posteroventral arms (pv a) and circlet of hooks. (Govetts Leap). Scale bar = 0.2 mm. **FIGURE 98.** (98) Typical habitat of *A. strenua*. (Souita Falls), Queensland. Image courtesy Waterfalls of Oz.

Victoria: Warburton, Cement Creek, S37.7239° E145.7542°. 1 April 1972. Larvae. Coll. Zwick (ANIC). Narbethong, Anderson Lane, Stony Creek, S37.54607° E145.6546°. 22 Oct. 2014. Reared males. Coll. D.A. & R.E.G. Craig (UASM).

Remarks. *Austrocnephia strenua* is a distinctively large species and was so noted by Mackerras & Mackerras (1950: 170). Apart from the large size, in particular that of the larvae, the adults are brightly coloured on the thorax and have pigmentation on the wings. The male eyes have reduced rows of large upper ommatidia, thought at the time to be unique in Australian Simuliidae (Mackerras & Mackerras, 1950: 170). That, however, was mainly because most simuliid species in Australia were then described from female adults. This feature of the males is now

known to be common for *Austrocnephia*. Large upper ommatidia are reminiscent of some species of *Gomphostilbia* Enderlein, such as *Simulium* (*G.*) *laciniatum* Edwards, of Fiji. The markedly domed thorax in both male and female *A. strenua* adults is also well expressed elsewhere in the genus.

There is considerable variation in the degree of tuberculation on pupal abdominal tergites. We illustrate the condition from Bartle Frere (Fig. 87) where it is well expressed. Tubercles, however, are absent from Lamington National Park material and elsewhere. Similarly there is variation in the development of the spinous teeth of the larval mandible. Colbo (1974: 68) noted that South Queensland larvae differed from northern larvae in having a different pattern of microtrichia on the labral fan rays, plus the prothoracic proleg lappet expression was slightly different. The variation in character states in different populations (Fig. 196) of *A. strenua*, such as teeth on the one or other sides of the female mandible, differences in the apex of the male ventral plate (Fig. 76 vs. 78) from that illustrated by (Mackerras & Mackerras, 1950. Their Fig. 3), pupal gill filament number, tuberculation on the pupal abdomen, serrations on the larval mandible, and those mentioned previously, well indicate that as presently defined, *A. strenua* is likely a complex of closely related entities. There are, indeed, considerable distances between different populations, particularly those to the south. Since, however, we lack complete material from such populations, we refrain from designating new taxa.

Palmer & Craig (2000) examined total number of hooks comprising the posterior circlet in larvae of simuliids in relation to velocity of preferred habitat. Such a correlation was noted by Mackerras & Mackerras (1950: 172) for *A. strenua* and for other simuliid larvae by Crosskey (1990: 110), Adler *et al.* (2004: 58) and Figueiróa *et al.* (2015), amongst others. Inhabiting extreme velocity flow, an expectation would be that *A. strenua* might perhaps approach the record number of hooks known for simuliid larvae. While numerous (*ca.* 17,200), hooks do not approach numbers exhibited by larvae of *Freemanellum* Crosskey species (Palmer & Craig, 2000: 202), or of those of *Daviesellum* Takaoka & Adler (Takaoka & Adler, 1997: 18), larvae of which inhabit jets of water impinging on rocky surfaces.

There are a number of other character states of larvae and pupae that appear to directly relate to the extreme high velocity habitats, *e.g.*, Souita Falls (Fig. 98)—firstly, the substantial nature and size of the larvae. Mackerras & Mackerras (1950: 172) commented that the body was very muscular. The anal sclerite is markedly developed with the posteroventral arms paralleled by the posterolateral arms arising from the medial region of the anal sclerite. Further, there are numerous campaniform sensilla between the posterior arm and the circlet of hooks—in other simuliid larvae they generally number four or so. The circlet of hooks is also markedly developed with number of hooks considerable and expression substantive; again fitting well with the extreme habitat. Further, unique to *Austrocnephia*, and in particular *A. strenua*, is possession of two anterolateral structures on the prothoracic proleg (Fig. 95). As noted previously, these were termed ‘palp-like processes’ by Mackerras & Mackerras (1950: 172), and ‘lappets’ by Colbo (1974: 69)—we use the term ‘lappets’. The proleg also has well expressed L-shaped lateral sclerites and the lappets arise from the internal apices of those, but while the lappets are often pigmented, they are not well sclerotised. Neither does there appear to be any muscular attachment. What function these lappets serve is unknown. Less well developed lappets can occasionally be observed in *A. aurantiaca*, *A. orientalis* and *A. tonnoiri*, but have not been observed in larvae of *A. fuscoflava*. Homologies of the lappets is moot. Van Oye (1936) illustrates a possible homolog, albeit on the prothoracic proleg of *Simulium* larvae. For pupae of the *aurantiaca* species-group, cuticle is well sclerotized and cocoon silk markedly strong.

Forming aggregations for aquatic organisms in high velocity flow is a well-known ploy to ameliorate drag forces (*e.g.*, Nowell & Jumars, 1984: 317; Craig, 2003: 1087). In such an arrangement the boundary layer of the water lifts and flows over the aggregation rather than around or between individuals, thereby reducing drag and is known as ‘skimming flow’. However, consequences of such behaviour are probably that for larvae, packed close together, individuals must be elongated and labral fans well expressed to access particulate matter. Indeed, an expanded posteroventral abdomen (Fig. 88) appears characteristic of simuliid larvae that inhabit fast flows (*e.g.*, Craig, 1987a: 396). Similarly, clumped pupae achieving skimming flow would still require the gills to be exposed to flow and thence the cocoons are stacked, with only the posterior of the abdomen attached to the substrate, as noted here for *A. strenua* and some other members of the genus.

***tonnoiri* species-group**

Diagnosis Adults: smaller darker species, female total body length 2.2–2.9 mm; Rs neither thickened nor branched

distally; junction of r-m cross vein and R_1 with markedly expressed dark spot; pedisulcus more strongly developed as deeper furrowing of cuticle on dorsal base of hind tarsomere II; tarsal claw basal tooth a third or more length of main talon, claw heel slightly expressed; genital fork with anterior stem markedly broadened and bent; male gonostylus cone-shaped, with two apical spines; ventral plate apex broadly rounded, not markedly directed ventrally; parameres smaller. *Pupa*: gill with fewer (21–50) filaments; abdominal tuberculation slightly to markedly expressed; pleurites present on segments VI & VII. *Larva*: four to five hypostomal setae; lateral hypostomal serrations present; posterior tentorial pits small and rounded; prothoracic proleg lateral sclerite V-shaped; anal sclerite with posteroventral arms only; area between posterolateral arms and circlet of hooks with small number of campaniform sensilla; posterior proleg with markedly fewer (1,800–3,000) hooks; larvae occur in flows of various velocity.

***Austrocnephia fuscoflava* (Mackerras & Mackerras). New combination.**

(Figs. 99–132)

Cnephia tonnoiri fuscoflava Mackerras & Mackerras 1948: 236; original description.

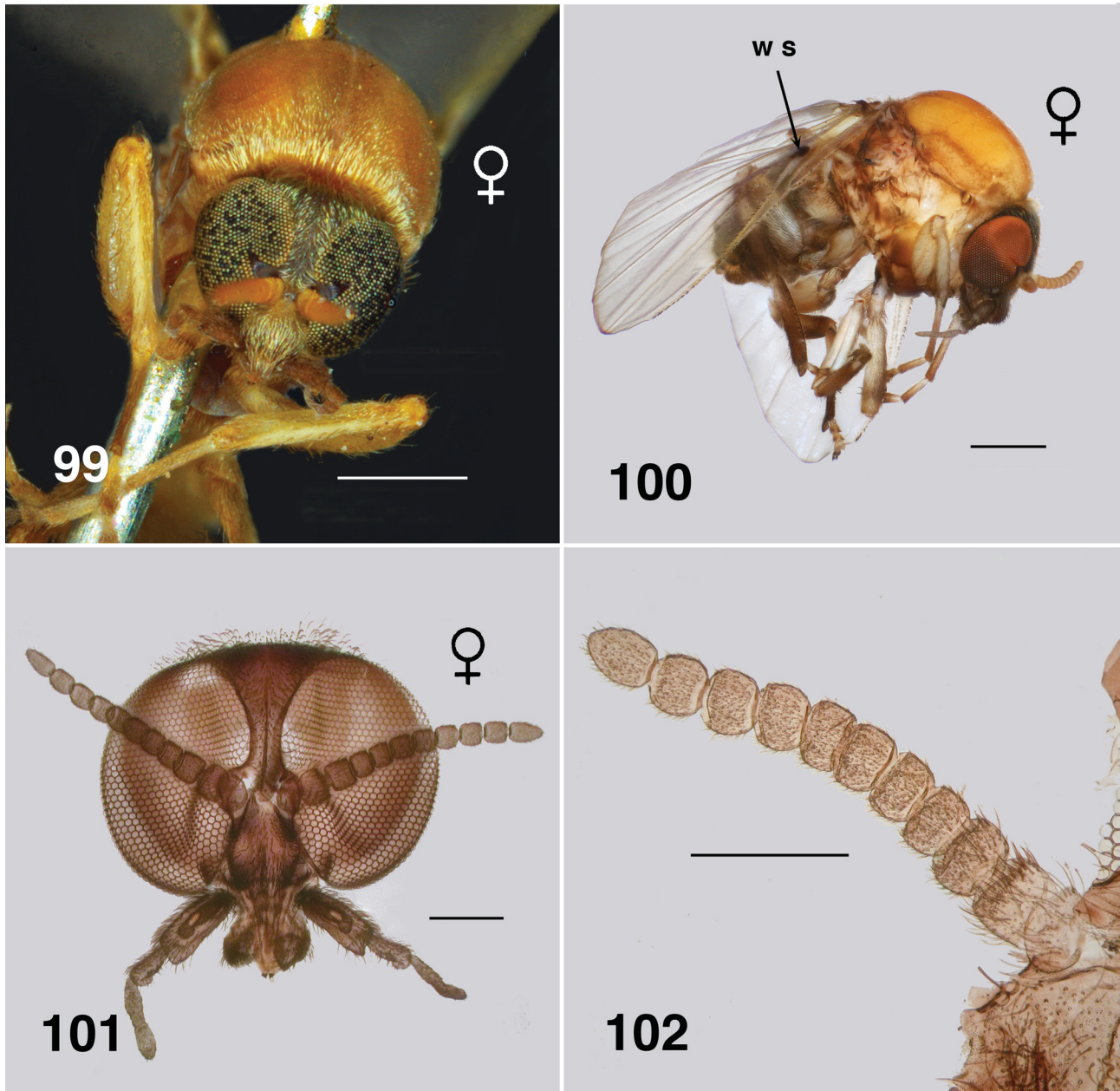
'*Cnephia* of authors' *fuscoflava*. Crosskey, 1987: 443.

fuscoflava. Crosskey, 1989: 222; unplaced species of *Prosimulinii*.

Paracnephia fuscoflava (Mackerras & Mackerras). Crosskey & Howard, 1997: 18; *Prosimuliini*, unplaced to subgenus, new combination. Bugledich, 1999: 328. Adler & Crosskey, 2008: 26, transferred to *Simulinii*. Adler, 2019: 32.

Redescription. *Adult female* (numerous reared specimens). A smaller species. *Body* (Figs. 99, 100): head very dark red, thorax tan, abdomen black; total length 2.2–2.4 mm. *Head* (Fig. 101): overall dark in colour; width 0.80–0.82 mm; depth 0.63–0.70 mm; postocciput markedly hirsute with long pale hairs, frons margins slightly concave, markedly narrowed, dark brown-black, sparse pale hairs; frons:head-width ratio 1.0:8.5–10.1. *Eyes*: interocular distance 0.08–0.09 mm; upper ommatidia redder than lower ommatidia, diameter 0.019 mm; lower ommatidia lighter in colour with slightly thicker margins, diameter 0.021 mm, *ca.* 36 rows across and 44 down at mid-eye. *Clypeus*: width 0.14–0.19 mm, markedly dark brown, densely hirsute. *Antenna* (Fig. 102): elongate, extended well beyond posterior margin of head; total length 0.63 mm; scape small and pale, pedicel larger and similar in size to flagellomere I, remainder similar in size, flagellomeres bead-shaped, concolourous, slightly tapered to apex. *Mouthparts*: feebly developed, *ca.* 0.23× length of head depth; maxillary palp, total length 0.70 mm, palpomeres I & II small, palpomere III darker brown than remainder with dense vestiture, palpomere IV small, V elongated; proportional lengths of palpomeres III–V, 1.0:0.7:1.6; sensory organ markedly elongated, 0.75× length of palpomere III, opening elongated and 0.6× vesicle width; mandible (Fig. 103) with *ca.* 26 small inner teeth, arrayed in straight formation (see insert), outer teeth absent; lacinia with 13 teeth on either side; cibarium cornuae flared with narrow terminal extensions, medial gap narrowed and concave, (Fig. 104). *Thorax*: length 1.3–1.5 mm, width 0.9–1.2 mm; scutum evenly tan; postpronotal lobe well developed with fine hair longer than on scutum, that with overall sparse fine small hairs; scutellar depression similar, concolourous, but with denser long pale hairs; scutellum slightly paler than scutum, vestiture of sparse very fine yellowish hairs centrally, darker laterally; postnotum concolourous with scutellum; anteppronotal lobe with distinct patch of yellow hairs; proepisternum and fore coxa bare; pleuron and anepisternal membrane yellowish brown, bare; katepisternum dark brown, sulcus shallow and broad. *Wing* (Fig. 105): length 2.5–2.8 mm; width 1.2–1.5 mm; very slightly fumose overall, veins yellowish, markedly developed pigmentation at junction of r-m cross vein as well as humeral and other basal cross veins; basal medial cell minute to absent; a:b ratio 1.0:2.4; distal 2/3 of costa with spines, dense apically, R_s not divided apically (Fig. 106); M_1 appears doubled; CuA barely sinuous; CuP extended nearly to wing margin, as does A_1 . *Haltere*: stem clear, knob tan. *Legs* (Fig. 107): forelegs evenly pale; mid and hind legs blackish brown; hind legs slightly darker; hind basitarsus parallel-sided with ventral row of stout spines; calcipala subequal in length and breadth, as wide as tarsomere; pedisulcus not markedly developed, but obvious; tarsomere II 2.0–2.3× longer than distal width; claws, smoothly tapered, not markedly curved, basal tooth well developed and broad, *ca.* 0.5× as long as talon, with distinct basal notch, heel small (Fig. 108). *Abdomen*: mottled dark brown overall, paler anteriorly; basal scale dark brown, vestiture of long dense hair extended to segment IV; tergites markedly poorly sclerotized, barely discernable from remainder of dorsum, broader in posterior segments; vestiture better expressed on posterior segments. *Genitalia*: markedly small; sternite VIII with no distinct medial region, vestiture of microtrichia, large strong hairs posterolaterally; hypogynial valves (Fig. 109), lightly pigmented, vestiture of triads of microtrichia and strong hairs, medial edges of valves slightly

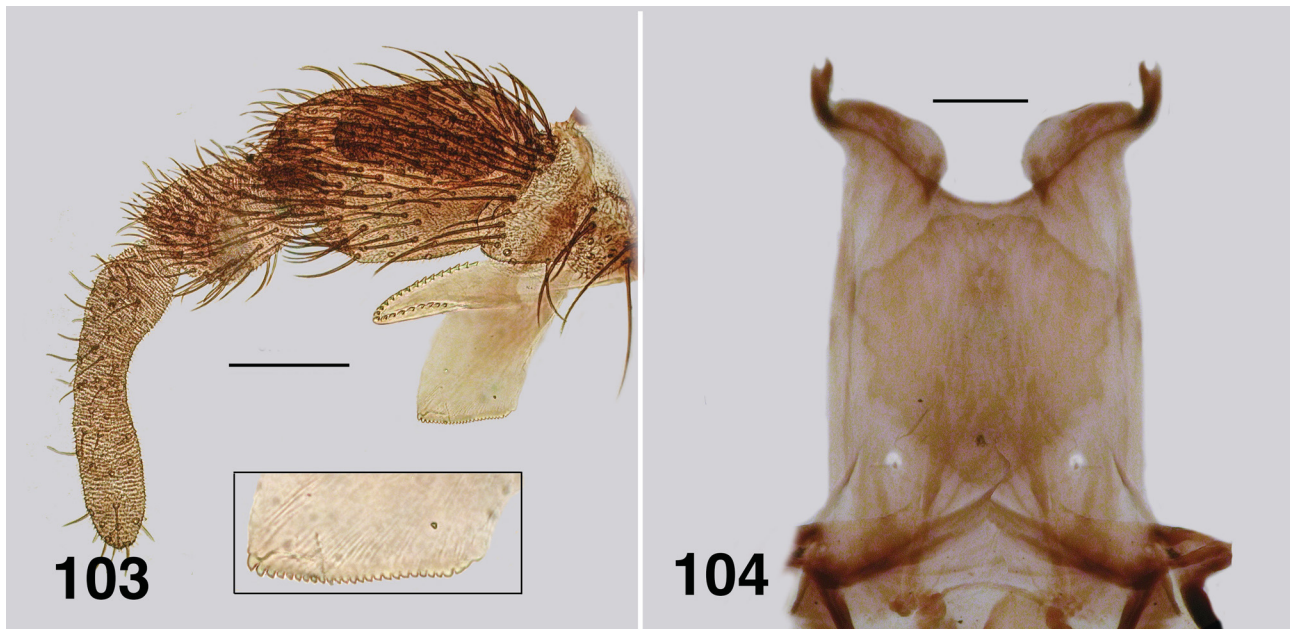
diverged—straight to slightly concave, bluntly triangular apically; cercus in lateral view elongated with faint medial depression, anal lobes smaller, with vestiture of long hairs (Fig. 110); genital fork (Fig. 111) well expressed, anterior arm thickened, flattened laterally, no indication of membranous lateral areas, lateral arms broad, no indication of knee-bend, apodeme absent, lateral plates triangular, small; spermatheca irregularly ovoid to spherical (Fig. 112), externally slightly tuberculate producing mottle effect, internal fine spines present, clear membranous area at junction with spermathecal duct small with series of raised cuticular rings.



FIGURES 99–102. *Austrocnephia fuscoflava* female. (99) Holotype, frontal view. (Stradbroke Island). Image by LHG-A. Scale bar = 0.5 mm. (100) Habitus. (Stradbroke Island). Arrow indicates wing spot (w s). Scale bar = 0.5 mm. (101) Frontal view of head. Paratype. Cleared. (Stradbroke Island). Scale bar = 0.2 mm. (102) Antenna. Paratype. Scale bar = 0.2 mm.

Adult male (numerous reared specimens, Stradbroke Island). *Body*: pinned (Fig. 113), head dark, thorax yellowish brown; in alcohol, overall colour darker, head dark red, thorax greyish brown, abdomen black (Fig 114); total body length 1.8–2.0 mm. *Head* (Fig. 115): width 0.83–0.84 mm; depth 0.83–0.86 mm; relatively large in relation to thorax. *Eyes*: upper ommatidia dark reddish orange, enlarged, diameter 0.05 mm, *ca.* 12–15 across and down; lower ommatidia black to blackish orange, markedly smaller, diameter 0.01 mm, *ca.* 26 across and down. *Clypeus*: black; width 0.17–0.18 mm; vestiture of fine black hairs. *Antenna* (Fig. 116): total length 0.59–0.67 mm; overall evenly light brown; scape short, pedicel as long as broad, flagellomere I longer than wide, flagellomeres II–V quadratic

in shape, apical three flagellomeres slightly longer than wide. *Mouthparts*: insubstantial; length $0.2\times$ head depth; maxillary palp 0.55 mm long, palpomeres I & II small, palpomeres III & IV subequal in length, palpomere IV elongated and as long as III & IV combined, proportional lengths of palpomeres III–V $1.0:0.8:2.0$, sensory vesicle small, spherical, occupying $0.2\times$ palpomere length, opening $0.33\times$ vesicle width; lacinia small, lacking teeth, but with apical hairs; mandible not observed. *Thorax*: markedly domed, lateral outline semicircular; length 1.1 mm; width 0.9 mm; postpronotal lobe with longish fine pale hairs, anteppronotal lobe with patch of sparse fine pale hairs, proepisternum bare; scutum evenly greyish yellow (tan), vestiture of evenly sparse longish fine pale hairs, longer anteriorly and in scutellar depression; scutellum yellower than scutum with markedly long yellow hairs laterally, postpronotal lobe concolourous with scutum; pleuron greyish yellow, anepisternal membrane bare, katepisternum dark brown, sulcus distinct, but shallow. *Wing*: length 2.8 – 2.9 mm, width 1.1 – 1.3 mm; membrane slightly fumose at apex; a:b ratio $1.0:2.6$; veins slightly yellowish, costa with well expressed spines, more so distally, r-m cross vein junction darkly pigmented, as are basal humeral and other cross veins (appear as two spots), Rs shows no sign of bifurcation or thickening distally, M_1 thickened and appears slightly doubled, CuA slightly sinuous, CuP extended nearly to wing margin. *Haltere*: stem pale, knob tan. *Legs*: overall bicoloured, pale and black, hind leg with tibia darker coloured distally; hind basitarsus margins parallel; ventral row of stout spines, sparse; calcipala well developed, narrower than basitarsus, with deep dorsal notch; pedisulcus not markedly developed; tarsomere II $2.3\times$ as long as apical width; tarsal claw small and finely expressed, with truncated basal tooth and smaller basal projection, grappling pad of *ca.* 23 teeth (as for other species). *Abdomen*: black dorsally and posteriorly, pale anteroventrally, vestiture of markedly long golden hairs, more so anteriorly; basal scale not markedly pigmented, hairs golden, extended to posterior of tergite II; tergites not markedly sclerotized, increased in width posteriorly and more fully pigmented; pleural cuticle concertinaed; sternites moderately developed, sternite II absent. *Genitalia* (Fig. 117): small, not heavily pigmented; cerci well developed and distinct; gonocoxa, in ventral view, $2.3\times$ longer than basal width, strengthened posteromedially, extended beyond junction with gonostylus, vestiture of long black sparse hairs, microtrichia, posteromedial margin scalloped; gonostylus short, in ventral view curved, in lateral view cone shaped (Fig. 118), approximately $1.5\times$ longer than basal width, strengthened along inner edge, two insubstantial short, blunt, apical spines; ventral plate (Fig. 119) small, $2.0\times$ wider than long, posteromedial apex directed slightly ventrally, appearing as shallow medial concavity, curved laterally, slightly convex anteromedially, vestiture of sparse coarse hairs medially, basal arms finely expressed, paramere connection not markedly expressed; median sclerite poorly expressed—two widely separated short sclerotized arms projected ventrally; parameres plate-like, lightly expressed, slightly crenulated along inner edge, spines absent; aedeagal membrane adorned with microtrichia.



FIGURES 103, 104. *Austrocnephia fuscoflava* female. (103) Maxillary palp, lacinia and mandible. Insert—mandible apex. Paratype. Scale bar = 0.1 mm. (104) Cibarium. Scale bar = 0.1 mm.

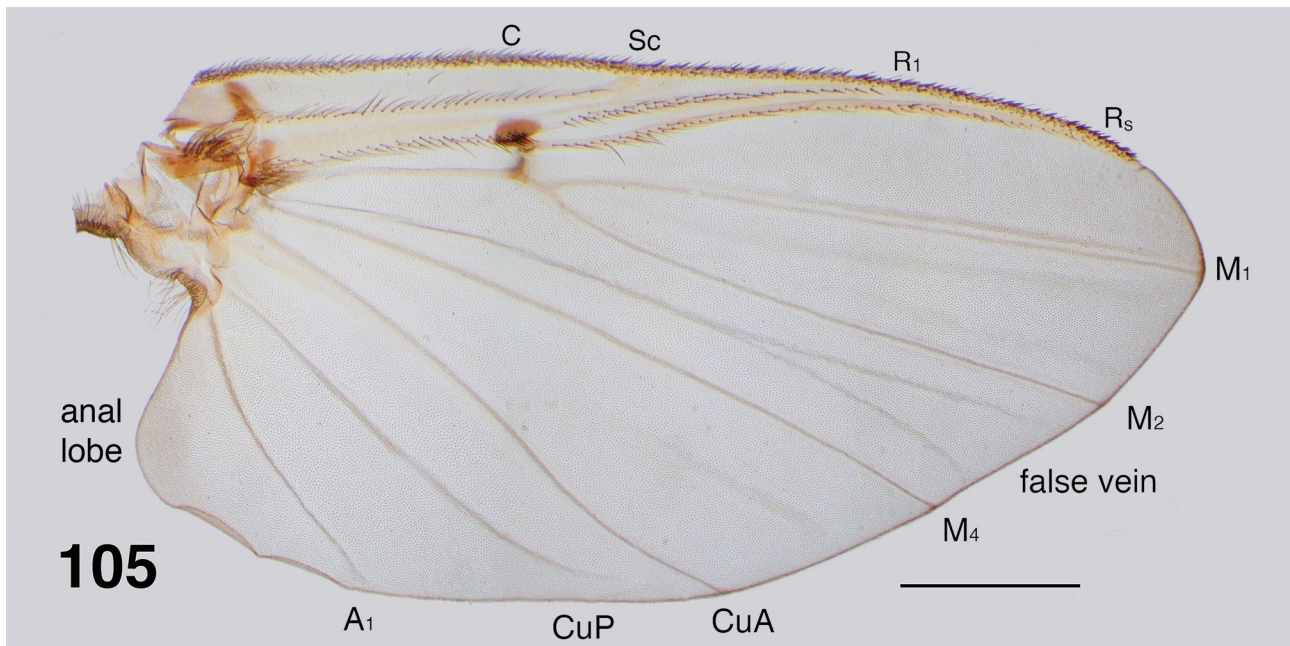
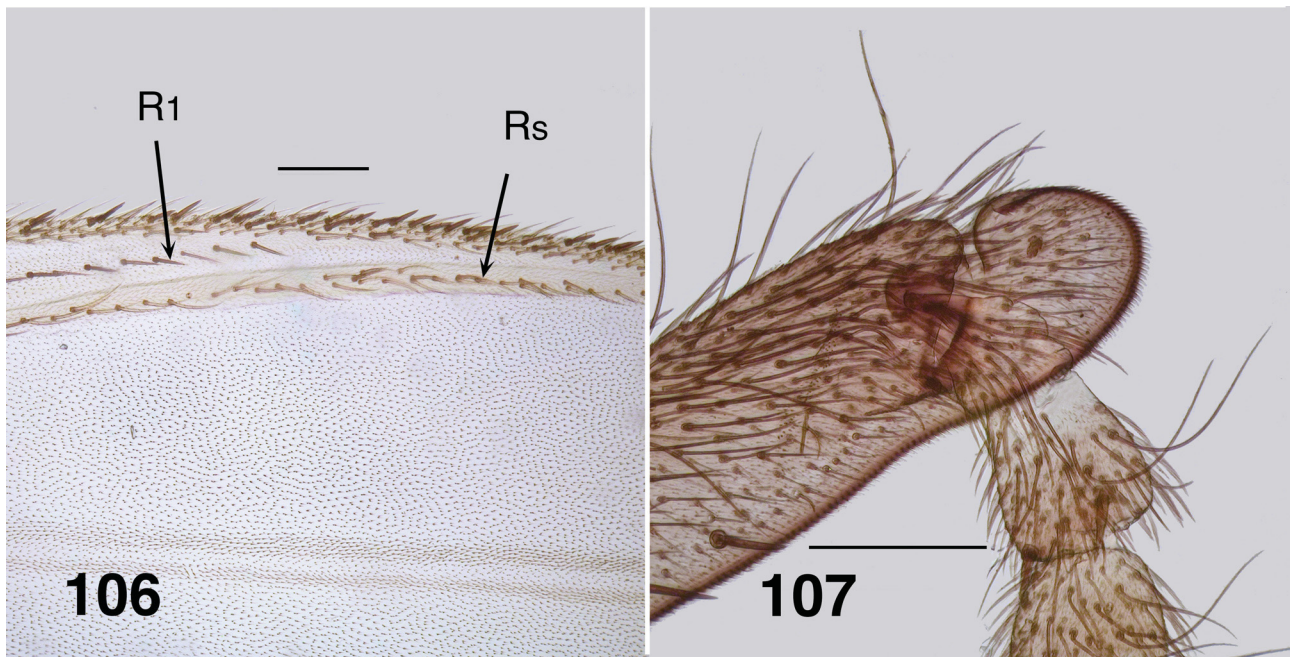
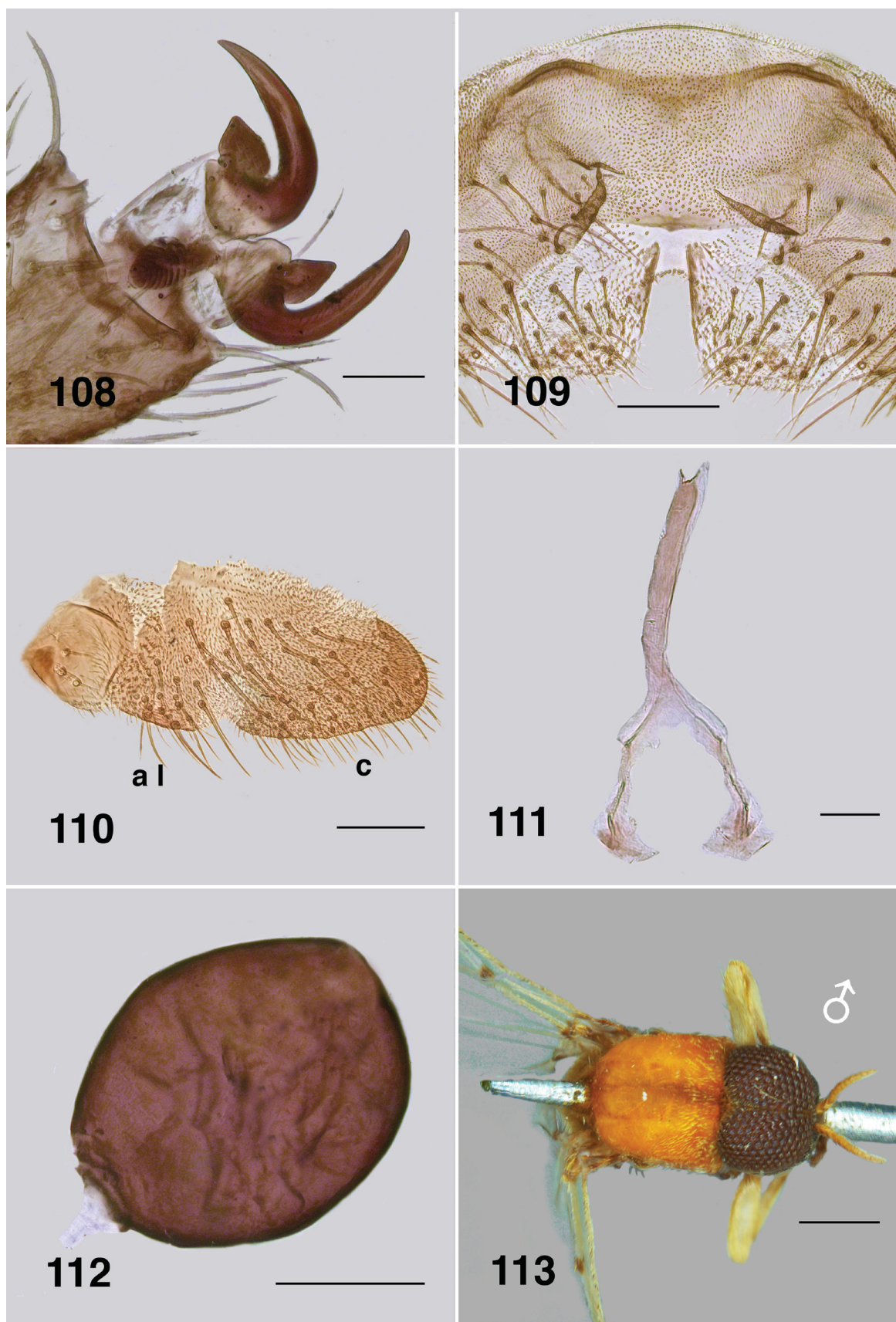


FIGURE 105. *Austrocnephia fuscoflava* female. (105) Wing. Paratype. Scale bar = 0.5 mm.

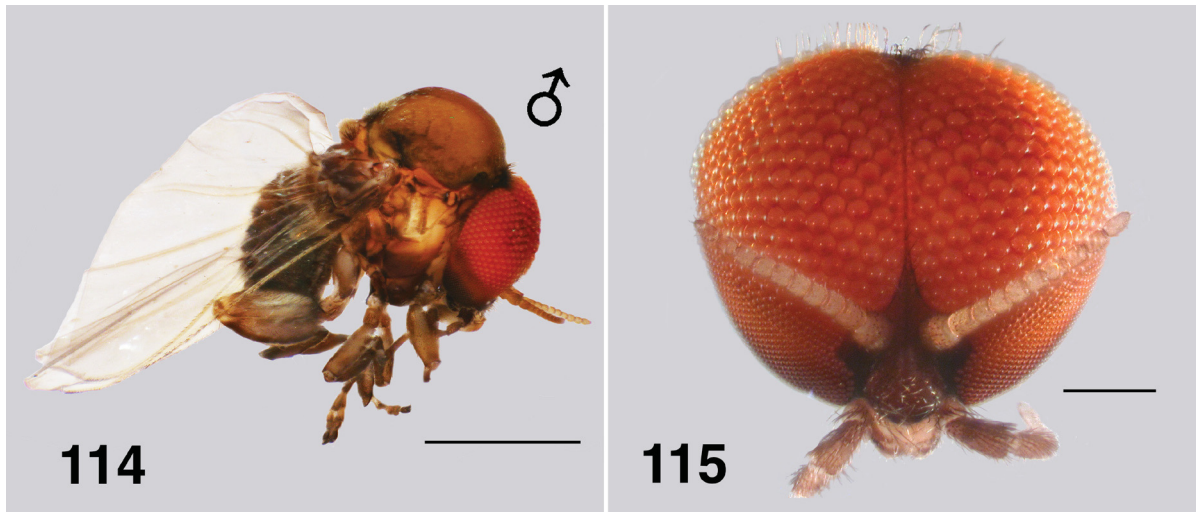


FIGURES 106, 107. *Austrocnephia fuscoflava* female. (106) Wing veins showing non-branched Rs. Scale bar = 0.1 mm. (107) Calypala and pedisulcus. Paratype. Scale bar = 0.1 mm.

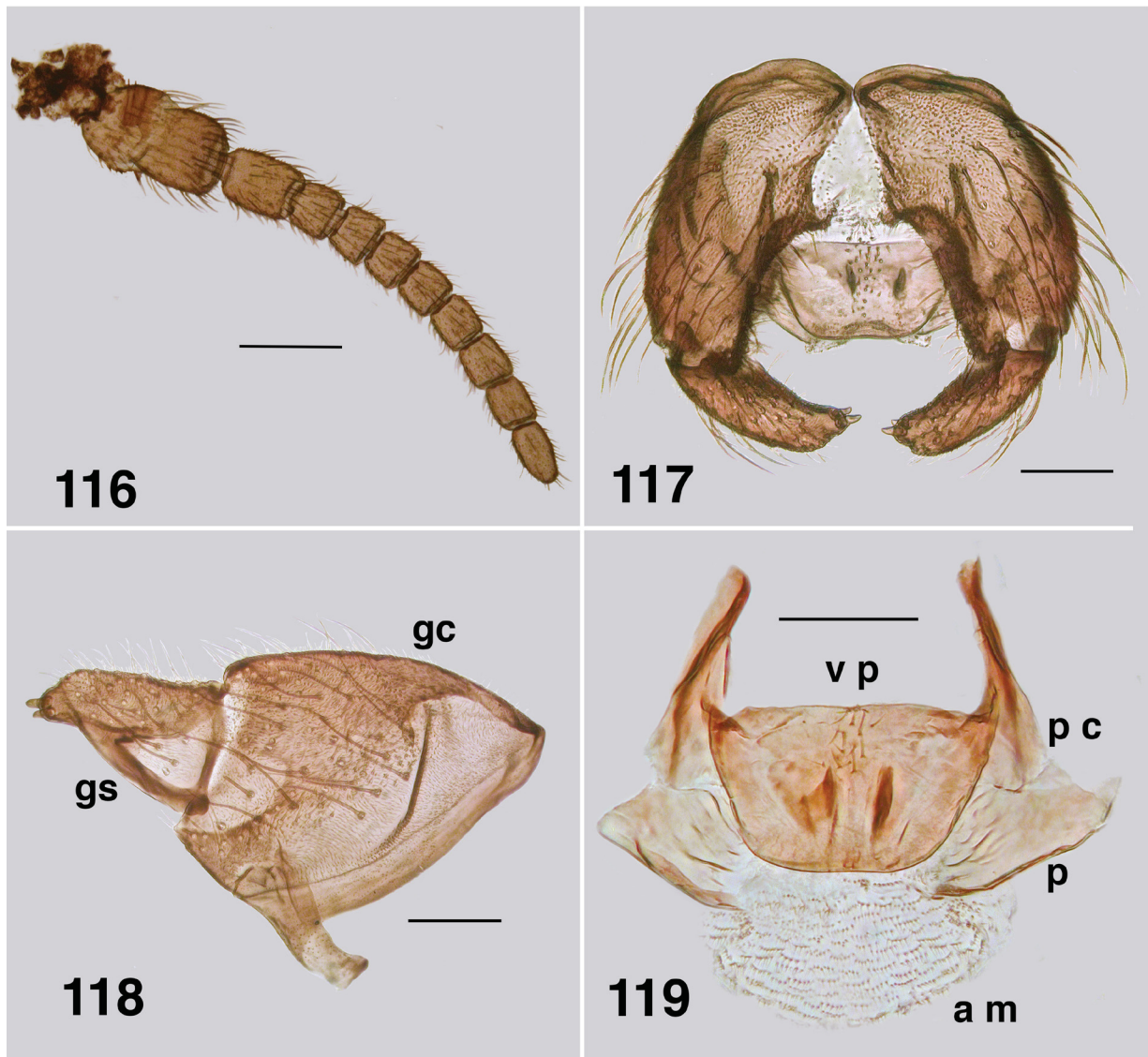
Pupa (based on numerous specimens). *Body*: female length 2.5–3.0 mm, male length 2.6–2.8 mm; clear yellow cuticle overall. *Head*: cephalic plates smooth, frons of female bluntly rounded with ratios of basal width to vertex width, and height 1.0:1.3 and 1.0:1.5 respectively (Fig. 121), male ovoid; ratios 1.0:1.7 and 1.0:2.7 respectively (Fig. 122); cuticle lacks pattern; in male, frontal and facial setae present, the former small and fine, the latter substantial and curved, in female facial setae present, frontal setae varied —either present on extreme lateral edge, or absent but on epicranial area; epicranial setae present, closely applied beside antennal sheath; antenna sheath of female extended beyond margin of ocular shield, not so in male. *Thorax*: notum markedly domed, smooth, but with faint pattern, dorsal setae short, substantial, curled at tip. *Gill* (Fig 123): total length *ca.* 0.75 mm; 15–20 brownish grey filaments arising from three or four short basal trunks, paler apically, arranged in antler-like fashion directed anteriorly; filament surface reticulated basally, pseudoannulated distally. *Abdomen* (Fig. 124): overall, cuticle clear



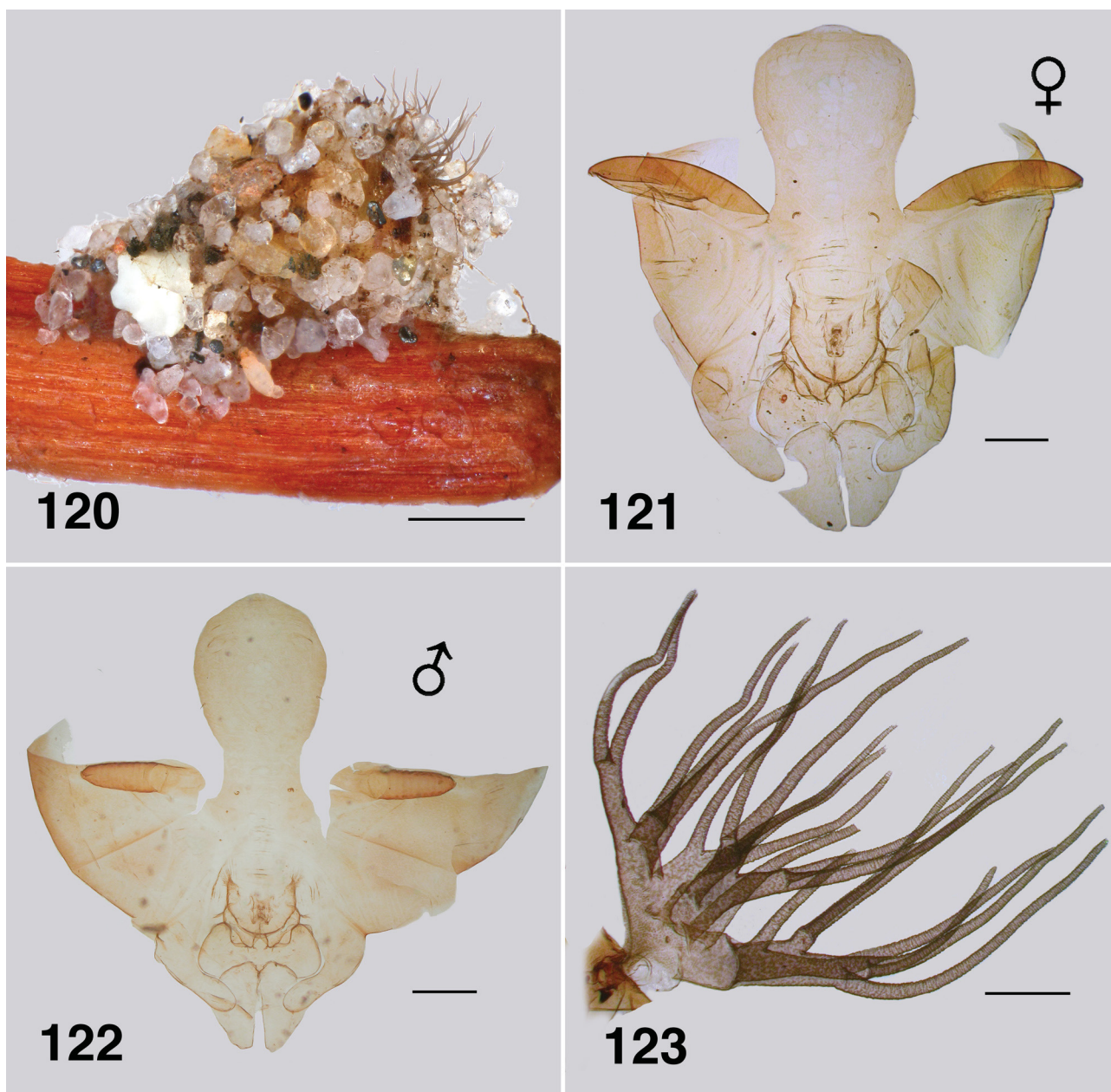
FIGURES 108–112. *Austrocnephia fuscoflava* female paratype. (108) Tarsal claws. Scale bar = 0.02 mm. (109) Hypogynial valves. Scale bar = 0.05 mm. (110) Anal lobe (a l) and cercus (c). Scale bar = 0.05 mm. (111) Genital fork. Scale bar = 0.05 mm. (112) Spermatheca. Scale bar = 0.05 mm. **FIGURE 113.** *Austrocnephia fuscoflava* male paratype. (113) Dorsal view. Image by LHG-A. Scale bar = 0.5 mm.



FIGURES 114, 115. *Austrocnephia fuscoflava* male. (114) Habitus. Scale bar = 1.0 mm. (115) Frontal view of head. Scale bar = 0.2 mm.



FIGURES 116–119. *Austrocnephia fuscoflava* male. (116) Antenna. Scale bar = 0.1 mm. (117) Genitalia, ventral view. Scale bar = 0.05 mm. (118) Gonocoxa (gc) and gonostylus (gs). Scale bar = 0.05 mm. (119) Genitalia, slide mounted, showing aedeagal membrane (a m), paramere connector (p c), paramere (p) and ventral plate (v p). Scale bar = 0.05 mm.



FIGURES 120–123. *Austrocnephia fuscoflava* pupa. (120) Habitus. Scale bar = 1.0 mm. (121) Female cephalic capsule. Scale bar = 0.2 mm. (122) Male cephalic capsule. Scale bar = 0.2 mm. (123) Gill. Tips of some filaments broken. Scale bar = 0.2 mm.

and well sclerotized, with distinct pale yellow sclerites, markedly so for anterior tergites; tergites III & IV connect to the respective sternites with wrinkled cuticle, no pleurites; but pleurites present and well expressed on segments V–VII, pleurite V larger and connected to both tergite and sternite, those of VI & VII smaller and isolated; sternites VI & VII separated medially; abdomen with minute rounded tubercles to absent. Abdominal armature moderately well developed; tergite I with fine hairs; tergite II with 4+4 poorly developed anteriorly directed hooks; tergites III & IV each with 4+4 central anteriorly directed long thin recurved hooks (similar to the ventral hooks), tergite IV with 1+1 lateral hooks, smaller than the more central hooks; tergites V–VIII each with spine comb anteriorly and posterior double pair of fine hairs on each side; segment IX with sharply tapered and slightly curved terminal spines, with other terminal setae simple, long and curved; sternite IV & V with 3+3 (2+2 stronger central and 1+1 poorly developed lateral); sternite VI with 2+2; sternite VII with 1+1 anteriorly directed simple recurved hooks; pleurites VI & VII with 1+1 anteriorly directed, poorly expressed, simple, recurved hooks.

Cocoon. Close fitting, may cover complete pupa, but variable in shape; irregular weave, silk fibers fine, dark brown; considerable extraneous material (algal filaments, sand, etc.) incorporated (Fig. 120).

Larva (based on numerous last instar larvae). *Body* (Fig. 125): total length 6.5–7.3 mm, evenly light grey and brown, markedly expanded posteroventrally. *Head* (Fig. 126): mottled medium brown, head spot pattern poorly expressed, but tending to positive; length 0.74–0.93 mm, maximum width 0.61–0.74 mm; distance between antennal bases 0.36–0.38 mm; apotome broad, ecdysial lines distinct and divergent until posterior of stemmata, cervical sclerites distinct, separate from postocciput and situated medially. *Antenna*: apex not extended to end of labral fan stem; total length 0.27–0.32 mm, overall brown; basal article short and clear proximally, darker brown distally, medial article and distal articles darker brown than remainder, basal article markedly shorter than medial article, proportional lengths of basal, medial, and apical articles 1.0:1.4:2.0, apical article relatively longer than others of the genus. *Labral fan*: stem short and broad, pigmentation ranging from pale to light brown, ca. 36–38 dark brown fine rays, ten posterior rays finer than others, length 0.8 mm, mid-ray width 0.01 mm; no microtrichial pattern as such—all of similar length (0.02 mm) and markedly longer than ray width. *Mandible* (Fig. 127): well pigmented; brushes typical; outer teeth markedly short; apical tooth moderately developed; subapical teeth small and subequal in length, blunt; ca. 7 spinous teeth, first subequal in length to apical tooth, others slightly decreased in length proximally; serrations and sensillum well expressed; blade region slightly convex. *Maxilla*: heavily pigmented; palp cone-shaped, 2.6× as long as basal width; hair tuft at base of palp not markedly developed. *Postgenal cleft* (Fig. 128): shallowly V-shaped, with irregular anterior edge; postgenal bridge concolourous with genae. *Hypostoma* (Fig. 129): darkly pigmented; tooth 0 not prominent, but distinct, subequal to tooth 3, teeth 1 & 2 shorter and less prominent, tooth 4 longer and flanged medially, teeth 5–7 markedly small and not obvious, tooth 8 more basal, small and directed laterally; all teeth as a unit with parallel sides; serrations lightly expressed on convex lateral edge of hypostoma; four to six hypostomal setae on each side, anterior ones more substantial; ratio of hypostoma: genal bridge: postgenal cleft 1.0:1.5:0.7. *Thorax* (Fig. 130): gill histoblast broadly rounded with four or five substantial dark trunks visible basally, all directed ventrally then broadly posteriorly, then curled anteroventrally, with pale filament endings then turned dorsally along anterior edge of histoblast. *Prothoracic proleg*: well developed and elongated with sharply V-shaped lateral plates; lappets absent. *Abdomen*: evenly expanded from anterior to posterior segments, but markedly expanded posteroventrally at segments VII & VIII. *Rectal papillae*: three simple lobes, well developed. *Ventral tubercles*: absent. *Anal sclerite* (Fig. 131): anterior arms flared, strengthened laterally; main body of sclerite not markedly developed, posteromedial clear area open, posterolateral arms absent, posteroventral arms finely expressed and tapered, numerous campaniform sensillae anterolateral of posteroventral arm; seven or eight campaniform sensilla between the posteroventral arms and circlet of hooks; posteromedial extensions into circlet of hooks junction absent. *Posterior circlet*: well developed and directed posteriorly, ca. 130 row of hooks with 13–15 hooks per row (total ca. 1,820).

Eggs. Laid in mats on trailing grass. Typical triangular shape.

Etymology. Not expressly given by Mackerras & Mackerras (1948: 236), but no doubt in reference to the tan colour (dark blonde) of the adult scutum.

Types. *Holotype*. The female holotype (ANIC) was examined and photographed by LHG-A in 2007 (Fig. 99). Exact labeling not recorded. The type locality (Mackerras & Mackerras, 1948: 236) is merely given as “Dunwich, Stradbroke Island”; the original collection was by E. N. Marks, 28 Nov. 1947. Stradbroke Island is also now known as ‘Minjerribah’.

Paratypes. Bugledich (1999: 328) listed 10 male and nine female paratypes in the ANIC with two male and two female specimens in the Natural History Museum, London. There were 16 ANIC specimens available for our examination, including six paratypes:—three males [Dunwich/ em. 12 Oct. 47] [Cnephia/ tonnoiri fuscoflava/ M&M/ PARATYPE. {male symbol}] [Aust. Nat./ Ins. Coll.] [ANIC Database No./ 29 031821–823]. The first numbered is now mounted on a microscope slide. Three females with data as for males, but with female symbol and [ANIC Database No./ 29 031824–03826]. The first is now mounted on a slide.

Additional material examined. Three pinned females [Dunwich, Q./ 11. 8. 51/ {female symbol}] [Aust. Nat./ Ins. Coll.]. A further eighteen (ANIC) slide mounts of all stages were examined, plus topotype material (Queensland Museum) and considerable newer material collected in 1996 by JKM, and that recently in 2015, collected by DCC and JKM. *Alcohol material*: All stages [ANIC Database No./ 29 026741–026744]; [UASM#/370832–370834]. *Slide mounts*: All stages [UASM#/ 370835–370846].

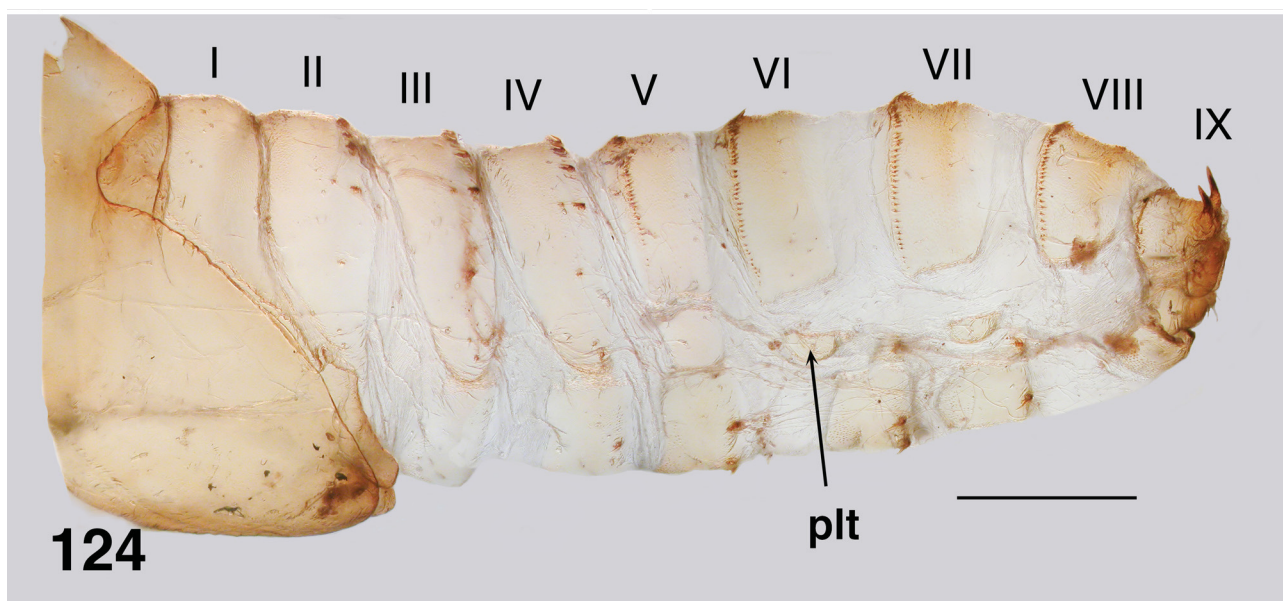
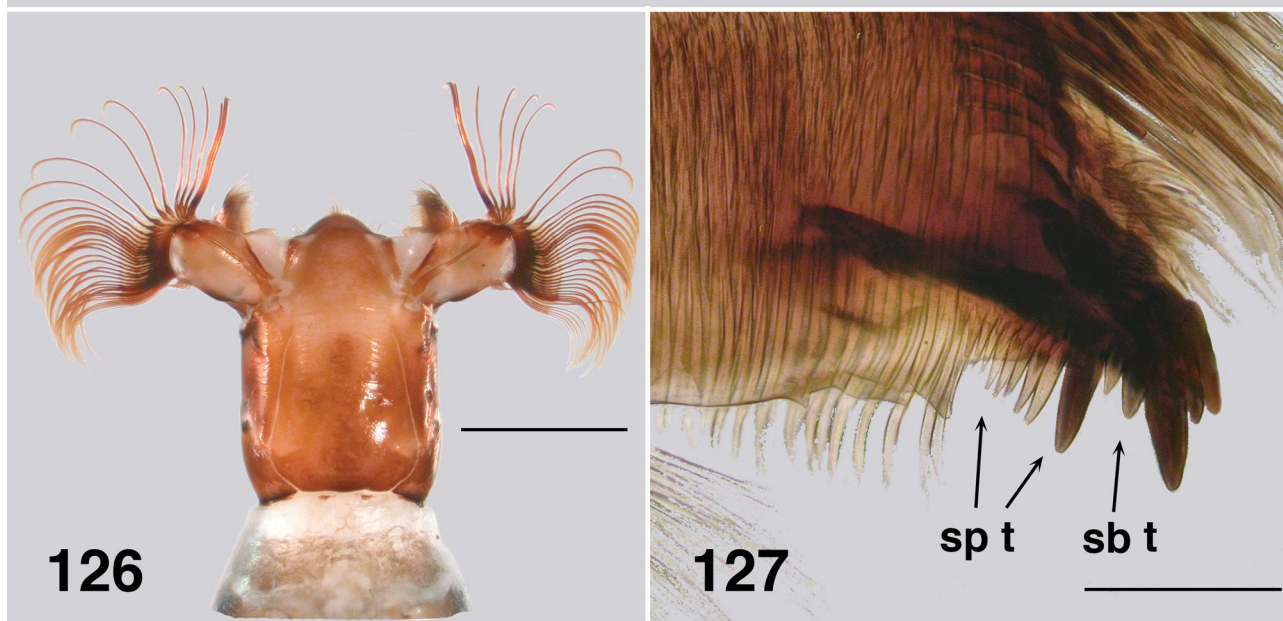
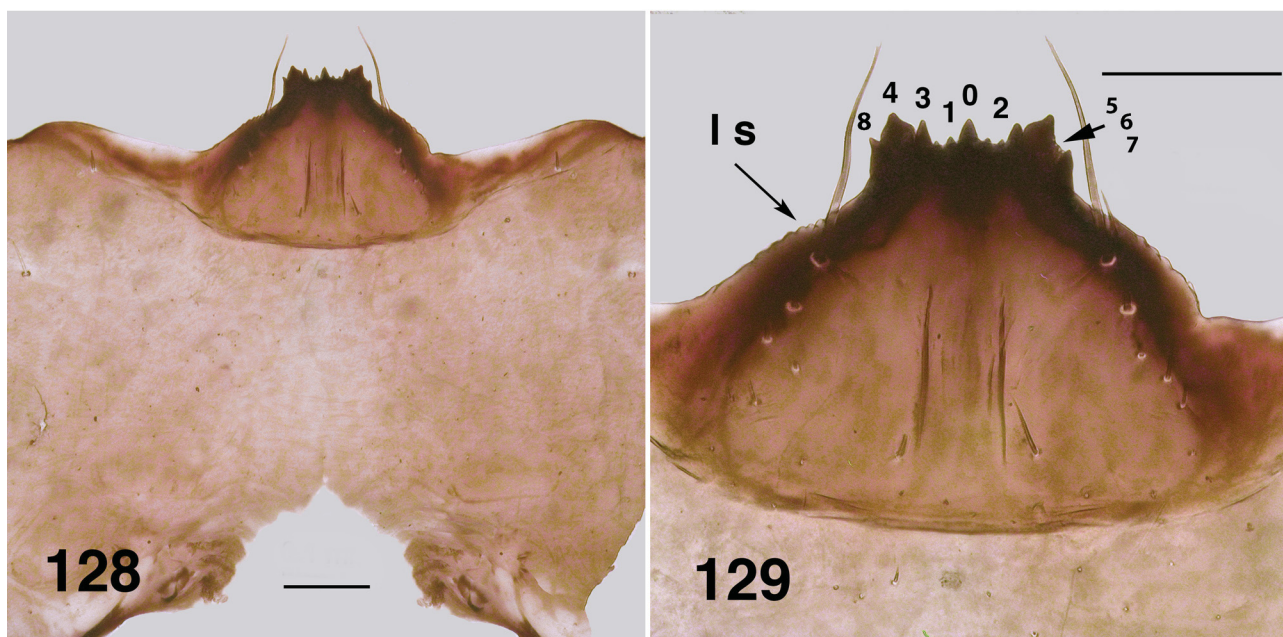


FIGURE 124. *Austrocnephia fuscoflava* pupa. (124) Abdominal armature. Arrow indicates pleurite (plt). Scale bar = 0.5 mm.



FIGURES 125–127. *Austrocnephia fuscoflava* larva. (125) Habitus, last instar. Scale bar = 1.0 mm. (126) Head, dorsal view, last instar. Scale bar = 0.5 mm. (127) Mandible apex showing subapical (sb t) and spinous (sp t) teeth . Scale bar = 0.05 mm.



FIGURES 128, 129. *Austrocnephia fuscoflava* larva. (128) Ventral head cuticle. Scale bar = 0.1 mm. (129) Hypostoma, note lateral serrations (l s). Scale bar = 0.1 mm.

Bionomics. In the original description, Mackerras & Mackerras (1948: 236) noted that eggs were unknown. We have examined, however, a sample collected in 1951: the eggs are laid as a mat on grass leaves and are of normal triangular shape. Mackerras & Mackerras (1948: 239) further noted that larvae of all ages were abundant in clear, moderately fast, somewhat brown water flowing in a narrow man-made channel, plus in a small, sunlit, natural stream just before it discharged onto a beach, both streams with sand substrate. Larvae were attached to vegetation, submerged sticks and logs, and especially to barely-submerged long grass blades. Pupae were in similar situations as the larvae and covered by irregular cocoons with extraneous material incorporated (e.g., Fig. 120). This is a notable feature for pupae of this species. No adults were originally collected from the type locality and there were no records of any biting. Given that Stradbroke Island is a tourist location and biting, as far as known, not been reported, the species may be autogenous, or highly ornithophilic as are most *Cnephia*-grade taxa.

More recent collections generally corroborate the original data. Of interest is that much of the newer material was collected from fast water (Fig. 132). Given collections from Stradbroke Island contain a full array of stages over an extended period of months, the probability that *A. fuscoflava* is multivoltine is high.

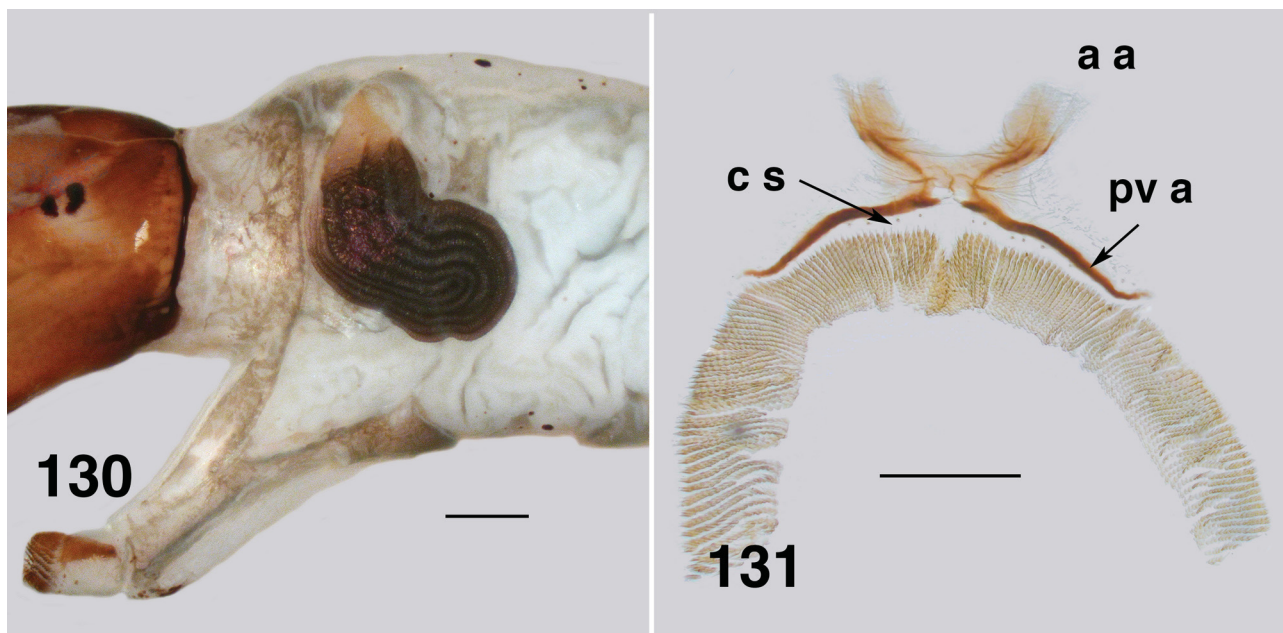
Distribution (Fig. 197). *Austrocnephia fuscoflava* was originally known only from Stradbroke Island (aka Minjerribah) near Brisbane (Mackerras & Mackerras, 1948: 236). No other simuliid species has been reported from the island. Bugledich (1999: 328) listed distribution of *A. fuscoflava* as widespread, from the NE coastal, SE coastal, NSW, QLD, TAS, VIC, but no such material is in the ANIC (DAC pers. obs., 2014). We assume that this given distribution is in error. Still, a single pupa collected by H. Zwick from Cement Creek, Victoria, was considered possibly that of *A. fuscoflava*. We have re-examined the specimen, but could not make a firm identification. Mackerras & Mackerras (1949: 384) gave Little Nerang River as a locality, but later (Mackerras & Mackerras, 1950: 170) retracted that. Moulton, however, collected *A. fuscoflava* material in 2002 from the mainland north of Brisbane, at Cooloola Creek, Rainbow Beach Road (S26.0050° E153.0590°), so the species is likely to occur elsewhere, but not as widespread as indicated by Bugledich (*loc. cit.*).

The exact position of the type locality is unknown. Moulton's 1996 Stradbroke material and that recently in 2015, collected by DCC and JKM was from Capembah Creek, Myora Springs Environmental Park (S27.4687° E153.4257°) (Fig. 132). The stream is generally with sandy substrate and of low gradient, but near the road there was a fast stretch and small waterfall that yielded specimens.

Remarks. Number of hooks (ca. 1,800) in the posterior circlet of the Stradbroke Island material is unusually low for the genus and in keeping with the lower velocity inferred for habitats of the original collections—streams

with sand substrates. As noted previously, this agrees with the correlation detailed by Palmer & Craig (2000) and others, regarding number of hooks and velocity of flow. That, as also noted elsewhere, is at variance with the abdominal shape—adapted for fast water.

An interesting point regarding slides prepared by the Mackerras's of the October 1947 material, is that some slides, originally labeled as *Prosimulium* sp., has that crossed out and relabeled *Cnephia tonnoiri fuscoflava*.



FIGURES 130, 131. *Austrocnephia fuscoflava* larva. (130) Pupal gill histoblast. Scale bar = 0.2 mm. (131) Anal sclerite showing anterior arms (a a), campaniform sensilla (c s), posteroventral arms (pv a) and circlet of hooks. Scale bar = 0.2 mm.

***Austrocnephia orientalis* (Mackerras & Mackerras). New combination.**

(Figs. 133–163)

Cnephia tonnoiri orientalis Mackerras & Mackerras 1950: 170; new subspecies. Mackerras & Mackerras, 1955: 105.

(‘*Cnephia*’ of authors) *orientalis*. Crosskey, 1987: 443; Prosimuliini, undetermined genus, raised to species status.

(Unplaced species of Prosimuliini) *orientalis*. Crosskey, 1989: 222.

Paracnephia orientalis. Crosskey & Howard, 1997: 18; new combination, unplaced to subgenus. Bugledich 1999: 328. Crosskey & Howard, 2004: 10.

‘*Cnephia*’ *orientalis*. Moulton, 2000: 98. Moulton, 2003: 47.

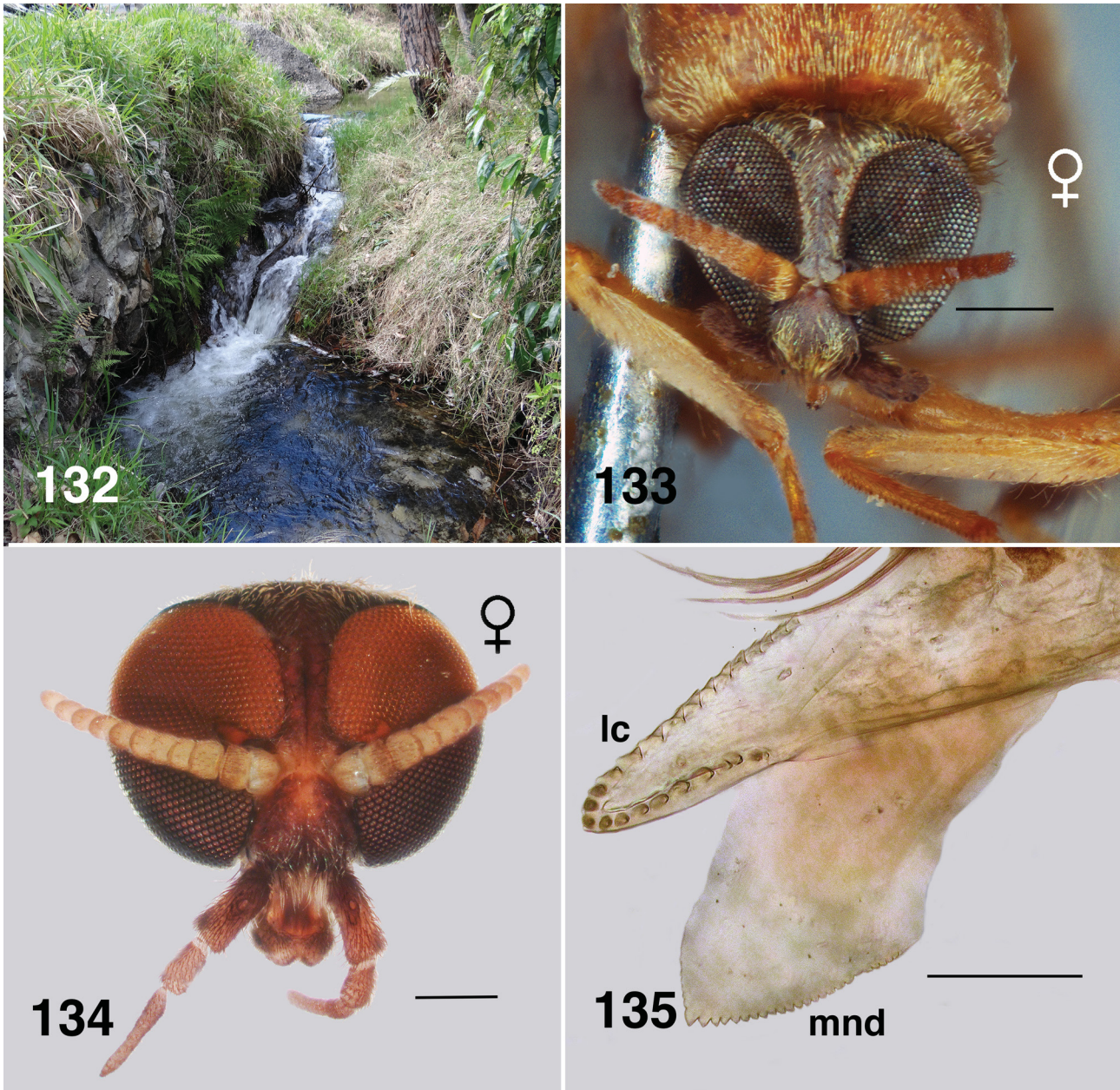
Paracnephia orientalis. Adler & Crosskey, 2008: 26; transferred to Simuliini. Hernández-Triana *et al.*, 2017: 350. Adler, 2019: 32.

Redescription. *Adult female* (based on holotype, slide mounts and numerous pinned specimens, ANIC). *Body* (Fig. 133): head and thorax yellow, abdomen black; total length *ca.* 2.8 mm. *Head* (Fig. 134): overall dark, width 0.98–1.00 mm, depth 0.70–0.80 mm; postocciput black, vestiture of dense hairs; frons narrowed basally, dark brown, slightly pollinose, vestiture of moderately dense silvery hairs; frons:head-width ratio various 1.0:9.7–12.4. *Eyes*: interocular distance 0.08–0.10 mm; ommatidia diameter 0.021–0.023 mm; *ca.* 37 rows across and 43 down at mid-eye, upper ommatidia slightly yellowish. *Clypeus*: width 0.14–0.30 mm; dark brown, vestiture of fine silvery hairs apically. *Antenna*: elongate, extended, but not markedly beyond posterior margin of head; overall pale brown; total length 0.62 mm; scape and pedicel subequal in size to flagellomere I, darker in colour; flagellomere I as wide as long, others broader than long, smoothly tapered to apex. *Mouthparts*: not markedly expressed, *ca.* 0.23× length of head depth; maxillary palp, total length 0.6 mm, palpomeres I & II small, III cylindrical, darker brown than others, dense vestiture, palpomere IV small, V elongated; proportional lengths of palpomeres III–V 1.0:0.6:1.4; sensory organ markedly elongated, 0.75× palpomere III length, opening elongated, 0.3× vesicle width, internally sensory organs numerous; mandible (Fig. 135) with *ca.* 25 poorly expressed inner teeth, minor serra-

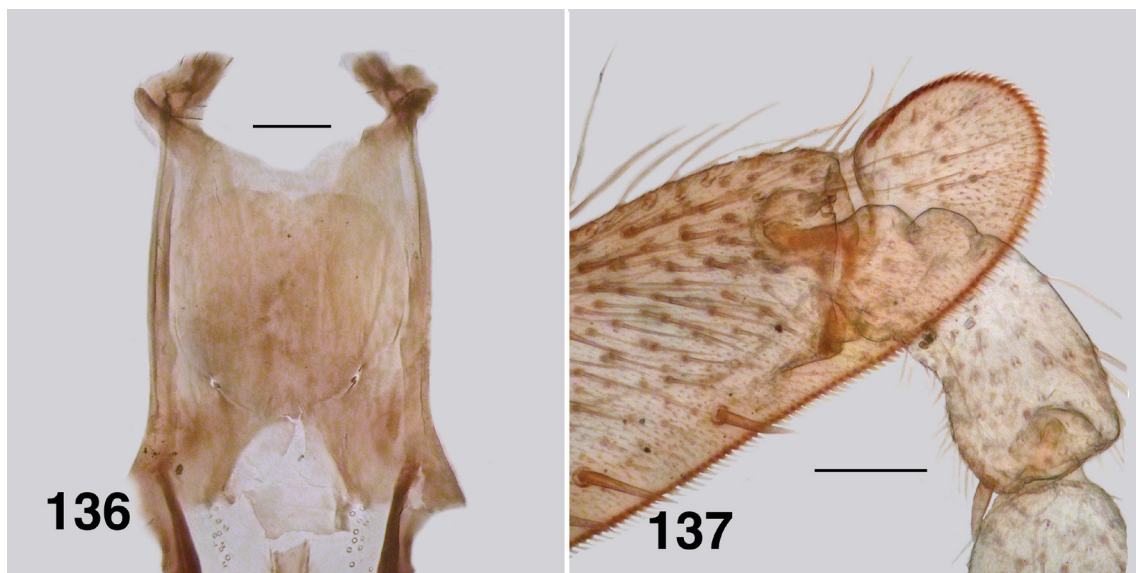
tions only on outer edge; lacinia with 15 and nine teeth on inner and outer sides respectively; cibarium (Fig. 136) cornuae slightly flared apically, medial gap shallow. *Thorax*: length 1.4 mm; width 1.1 mm; yellowish orange; postpronotal lobe well developed with dense fine hair longer than on scutum, scutellum slightly paler than scutum with vestiture of sparse very fine yellowish hairs; postnotum concolourous with scutellum, vestiture similar; antepronotal lobe haired; proepisternum and fore coxa bare; pleuron and anepisternal membrane light brown, bare; katepisternal dark brown, sulcus shallow and broad. *Wing*: length 3.3–3.7 mm; width 1.5–1.7 mm; membrane not noticeably fumose; basal medial cell minute; a:b ratio 1.0:2.3–2.7; distal 1/3 of costa with spines, Rs not divided distally, but slightly thickened (occasional row of hairs marks R_{2+3}), M_1 appearing doubled, but not markedly so; CuA not markedly sinuous; r-m cross vein junction with small distinct pigmented region; wing overall essentially as for *A. fuscoflava* (e.g., Fig. 105), but slightly blunter apically. *Haltere*: stem pale, knob darker. *Legs*: evenly yellowish brown; hind basitarsus with regular row of stout spines; calcipala markedly developed, subequal in length and breadth, distinct dorsobasal notch (Fig. 137); pedisulcus moderately developed; tarsomere II $2.0\times$ as long as distal width; claws with main talon smoothly tapered, basal tooth well developed, $0.3\text{--}0.5\times$ length of claw, distinct heel; overall essentially as for *A. fuscoflava* (i.e., Fig. 108). *Abdomen*: basal scale (tergite I) dark brown, vestiture of long dense yellow hairs, reaching well over tergite II; anterior few segments yellowish, other segments dark brown, dense vestiture of long yellowish hairs laterally and posteriorly; tergites overall markedly poorly sclerotized, each barely discernable from remainder of dorsum, hirsute, vestiture better expressed on posterior segments. *Genitalia* (Fig. 138): sternite VIII with distinct anterior edges and medial region, vestiture of microtrichia, large strong hairs posterolaterally; hypogynial valves, lightly pigmented, vestiture consists of triads of microtrichia and strong hairs apically, medial edges of valves slightly concave, minor strengthening anteromedially, moderately rounded apically; cercus in lateral view cone-shaped, with medial depression minute to absent, anal lobe small and rounded (Fig. 139); genital fork (Fig. 140) with anterior arm markedly strap-like in expression, strongly bent dorsally when emplaced (distorted in image), apically irregular, membranous lateral areas, lateral arms narrow, apodemes absent, posterolateral expansions small; spermatheca ovoid (Fig. 141) lightly pigmented, slightly wrinkled, without internal spines, clear region surrounding junction with spermathecal duct essentially absent.

Adult male (based on paratype, topotypes and other specimens). *Body*: pinned (Fig. 142), overall colour dark with yellow vestiture; in ethanol (Fig. 143) overall yellow and black; total body length 3.1 mm. *Head* (Fig. 144): width 1.1–1.2 mm, depth 0.8–0.9 mm. *Eyes*: upper ommatidia yellowish, markedly large, diameter 0.063–0.067 mm, 15–19 across and ca. 15 down; lower ommatidia black, markedly smaller, diameter 0.023–0.025 mm, ca. 35 across and down. *Clypeus*: black; width 0.16–0.20 mm; vestiture of sparse coarse black hairs. *Antenna*: barely extended beyond head margins; total length 0.63 mm; pedicel small, scape twice as long, rounded and dark brown, flagellomere I slightly narrower than scape, other flagellomeres tapered slightly to small apical flagellomere, all evenly pale brown; flagellomere I not as elongated as in *A. fuscoflava*, but overall as finely tapered. *Mouthparts*: markedly insubstantial; length $0.14\text{--}0.22\times$ head depth; maxillary palp 0.66–0.71 mm long, palpomeres I & II small, III & IV subequal in length, V elongated, proportional lengths of palpomeres III–V 1.0:0.8:1.8, sensory vesicle spherical shaped, occupying $0.25\times$ palpomere length, opening $0.5\times$ vesicle width; mandible and lacinia not observed. *Thorax*: markedly domed, head directed ventrally; length 1.5 mm, width 0.96 mm; postpronotal and antepronotal lobes with sparse longish fine pale hairs, proepisternum bare; scutum dark brown, vestiture of sparse short fine pale hairs, dense and long in scutellar depression; scutellum concolourous with scutum, bare medially, with sparse long pale hairs laterally; postnotum concolourous with scutum; pleurae brown, anepisternal membrane bare. *Wing*: length 3.3 mm, width 1.6 mm; otherwise as for female; Rs with no indication of branching. *Haltere*: base of stem pale, knob dark tan. *Legs*: overall yellowish brown; basitarsus with ventral row of stout spines, calcipala markedly developed and trowel-like; pedisulcus well developed; tarsomere II $2\times$ as long as distal width; tarsal claw as for other males in genus. *Abdomen*: overall yellow and black, basal scale hairs black, extended to posterior of segment IV, tergites poorly sclerotized, 3 to $4\times$ as wide as long, markedly hirsute, more so posteriorly; pleurites and sternites apparently absent. *Genitalia*: overall small and not heavily pigmented (Fig. 145); gonocoxa (Fig. 146) $1.3\times$ longer than its basal width, posteromedially strengthened and fluted, extended beyond articulation with gonostylus, vestiture of sparse hairs, microtrichia in rows, hairs accentuated medially, medial margin depressed and hirsute; gonostylus in ventral view narrowed, approximately $2.5\times$ longer than basal width, in lateral view markedly cone-shaped, $1.3\times$ longer than basal height, strengthened with clear smooth cuticle along one edge, two short blunt apical spines, the preapical one smaller; ventral plate small, simple (Fig. 147), $2.5\times$ wider than long, broadly rounded laterally, shallowly convex anteromedially, vestiture sparse to absent, basal arms broadly

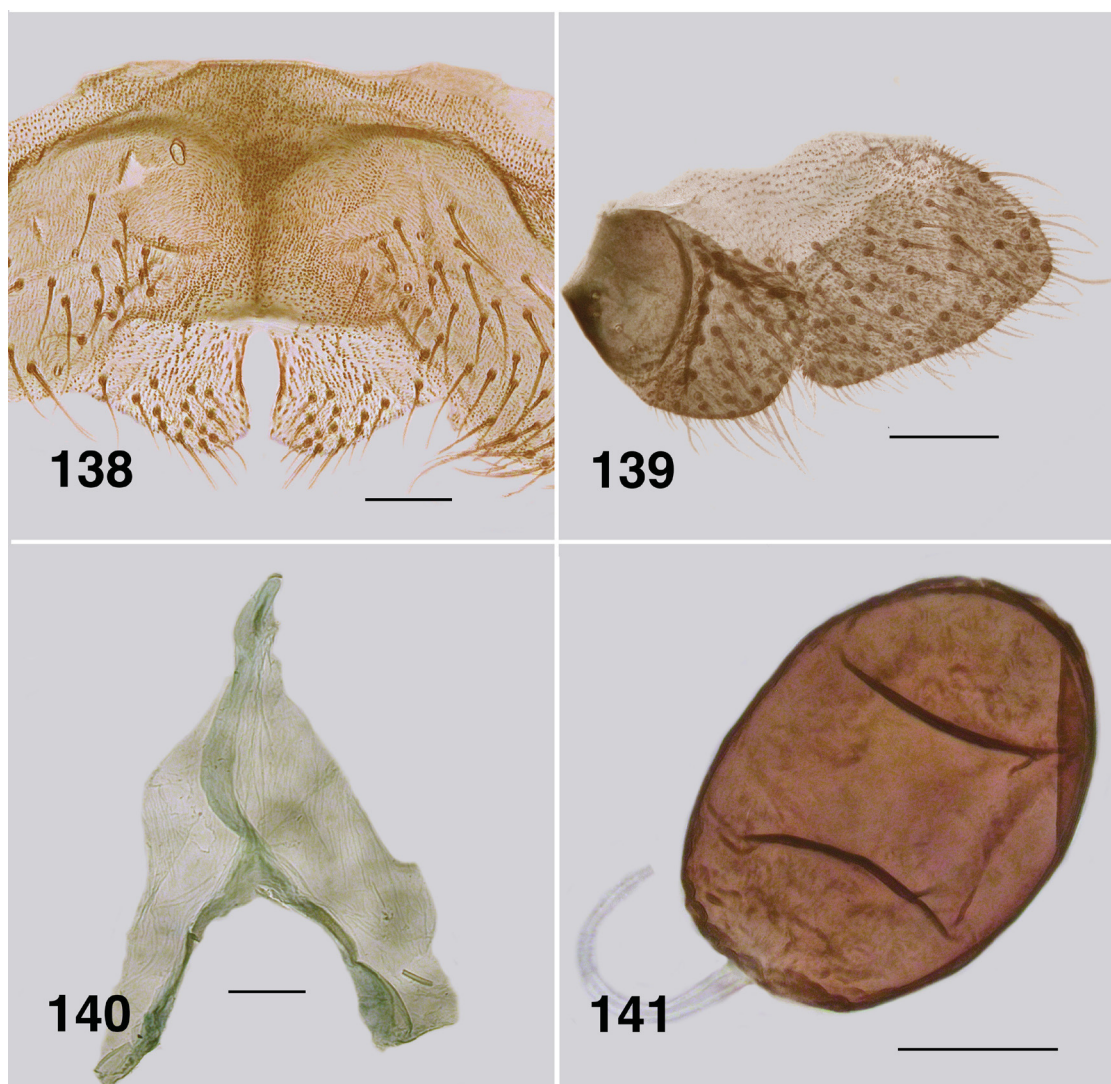
expressed, paramere connection small; median sclerite as for other species; parameres plate-like and bluntly triangular, slightly strengthened along one side, apex slightly fluted, spines absent; adeagal membrane with sparse microtrichia.



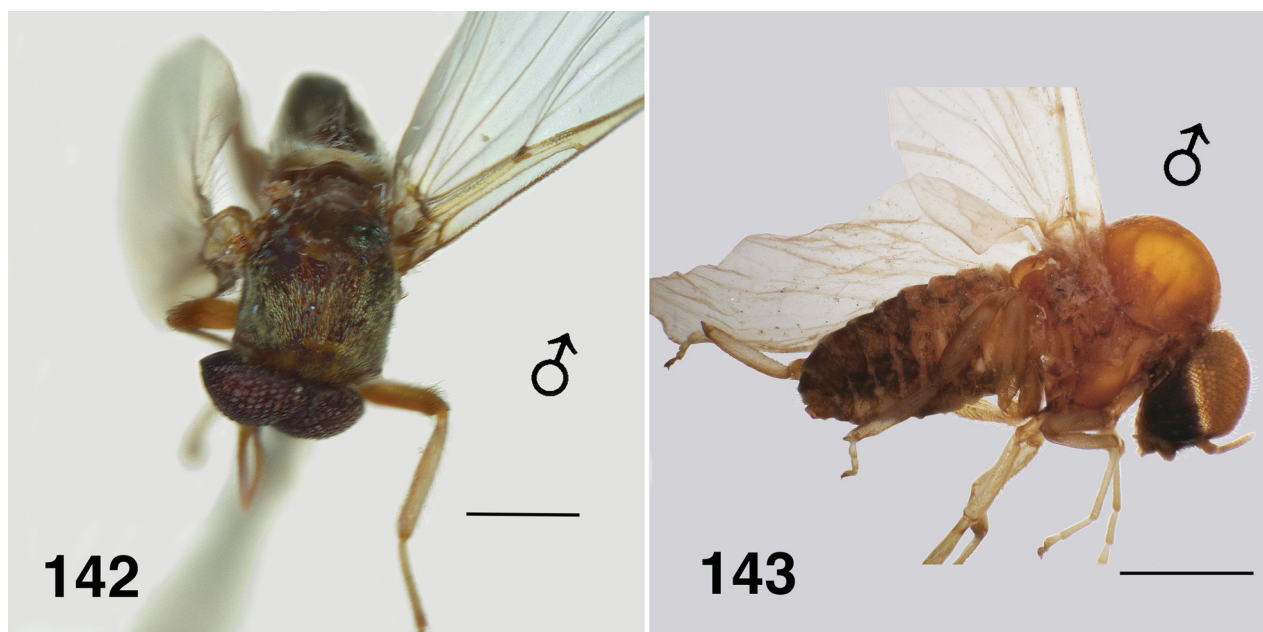
FIGURES 132. *Austrocnephia fuscoflava* larva. (132) Typical habitat of *A. fuscoflava* immatures. Capembah Stream, Stradbroke Island. Image JKM. **FIGURES 133–135.** *Austrocnephia orientalis* female. (133) Holotype, frontal view. Image by LHG-A. Scale bar = 0.25 mm. (134) Head. (Hume Highway). Scale bar = 0.25 mm. (135) Mandible (mnd) and lacinia (lc). (Hume Highway). Scale bar = 0.05 mm.



FIGURES 136, 137. *Austrocnephia orientalis* female. (136) Cibarium. (Springbrook). Scale bar = 0.05 mm. (137) Calcipala and pedisulcus. (Mt. Glorious). Scale bar = 0.05 mm.



FIGURES 138–141. *Austrocnephia orientalis* female. (138) Hypogynial valves. Scale bar = 0.05 mm. (139) Anal lobe and cercus. Scale bar = 0.05 mm. (140) Genital fork. Stained. Scale bar = 0.05 mm. (141) Spermatheca. Scale bar = 0.05 mm.



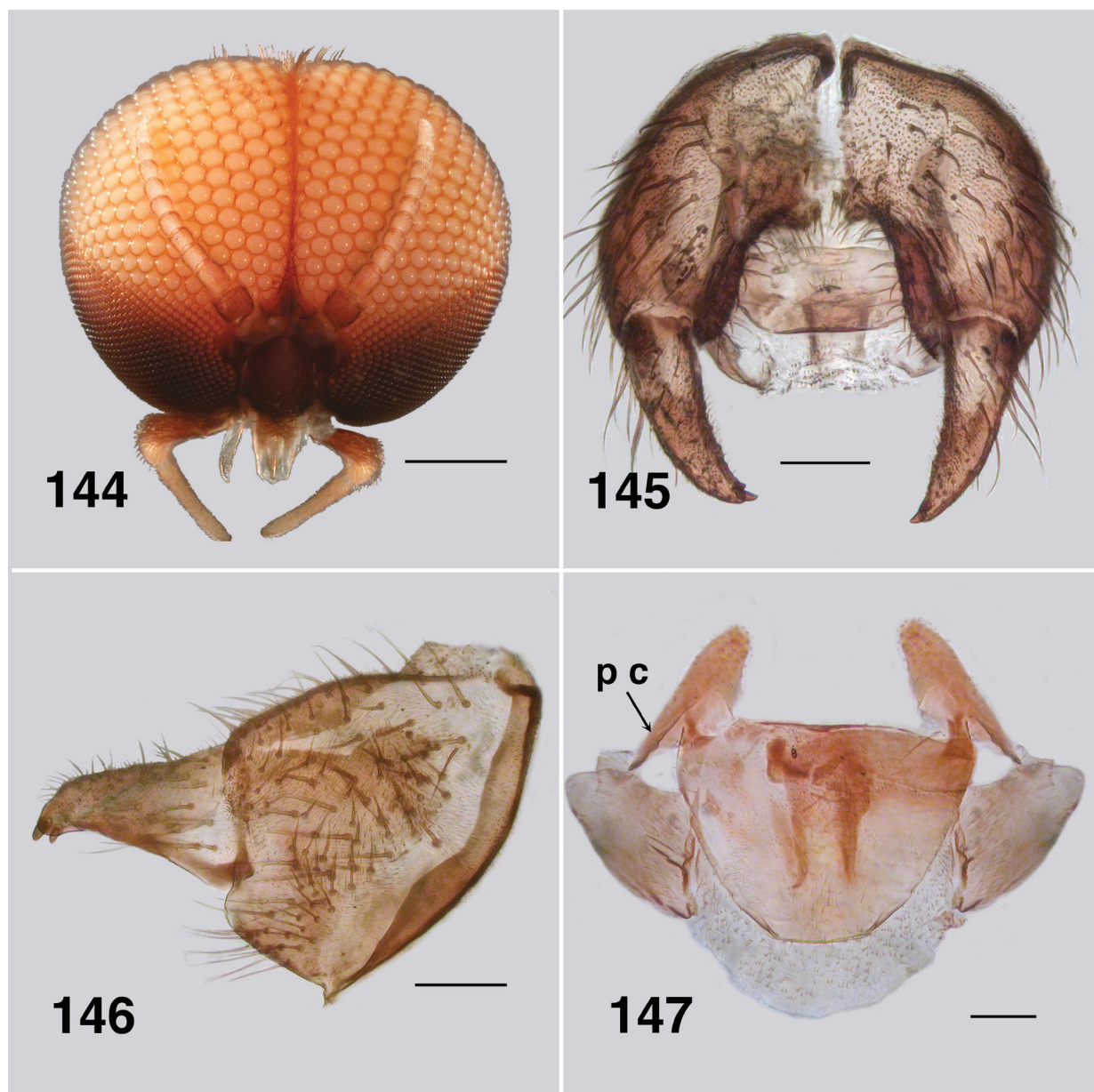
FIGURES 142, 143. *Austrocnephia orientalis* male. (142) Dorsal view. Paratype. (Little Nerang). Image by LHG-A. Scale bar 0.5 mm. (143) Habitus. Teneral. (Little Nerang). Scale bar = 1.0 mm.

Pupa (based on a small number of specimens). *Body*: female length 3.3–4.0 mm (Fig. 148), male length 3.3–3.8 mm, dark brown. *Head*: frons of female rounded; ratio of frons basal width to vertex width and height, 1.0:1.2 and 1:2.0 respectively (Fig. 149), that of male ovoid, markedly narrowed basally; ratios 1.0:2.0 and 1.0:3.0 respectively (Fig. 150); both smooth; in male, frontal and facial setae present, in female frontal setae absent, epicranial setae present, (in male well lateral of antennal sheaths, female under antennal sheath); two setal sockets anteromedial of tentorial pits; antennal sheath of female extended beyond edge of ocular shield, that of male markedly not so. *Thorax*: domed, smooth, dorsal trichoid setae curled at tip. *Gill* (Fig. 151): total length *ca.* 1.5 mm; 36–70 filaments arising from numerous short basal trunks (Mackerras & Mackerras 1950: 170, noted that the type locality and southern populations have lower numbers), some filaments bi- and trifurcate; light brown; surface with distinct fine annulations, albeit smooth apically (Fig. 152); tips pale and often broken. *Abdomen* (Fig. 153): armature as for *A. fuscoflava*, tuberculation markedly dense.

Cocoon. Close fitting, usually covering abdomen and occasionally part of thorax; irregular weave, silk fibers thick; often with extraneous material incorporated.

Larva (based on numerous last instar larvae). *Body* (Fig. 154): total length 5.6–7.2 mm, overall light yellowish brown, evenly expanded from anterior to posterior abdomen. *Head* (Fig. 155): evenly yellowish; head spot pattern poorly developed, but positive; length 0.85–0.89 mm, width 0.65–0.66 mm; distance between antennal bases 0.34–0.40 mm; anterior margins of head subparallel, straight; ecdysial lines not markedly visible, slightly concave until posterior of stemmata, then very broadly curved medially; cervical sclerites elongated and fused to postociput; genae brown. *Antenna*: not extended to end of labral fan stem; total length 0.33 mm; apical and medial sensillae small; basal article short and clear proximally, darker brown distally, medial article and distal articles evenly brown, subequal in length; basal article markedly shorter than medial article, proportional lengths of basal, medial, and apical articles 1.0:1.6:1.8; medial article of even diameter, or slightly diminished medially; otherwise as for *A. fuscoflava*. *Labral fan*: stem short and not markedly pigmented, *ca.* 34–36 dark brown fine rays, five posterior rays finer than others, length 0.66 mm, mid-ray width 0.013 mm; no conspicuous microtrichial pattern—most of similar length with longer ones (length 0.02 mm) at irregular intervals, ‘spines’ at base of ray not markedly developed, rather as series of short microtrichia and ill-defined serrations. *Mandible* (Fig. 156): various; darkly pigmented; short; apical brushes poorly developed; outer teeth short; apical tooth prominent; subapical teeth small and subequal in length; six or seven spinous teeth, distal one well developed; serration and sensillae moderately expressed; blade region straight. *Maxilla*: palp cone-shaped, varied, 1.6–2.1× as long as basal width, very dark; hairs at base of palp not markedly developed. *Postgenal cleft* (Fig. 157): shallow U-shaped; posterior tentorial pits small and rounded; postgenal bridge evenly light brown; elongated posteroventral muscles spots not markedly obvious. *Hypostoma*

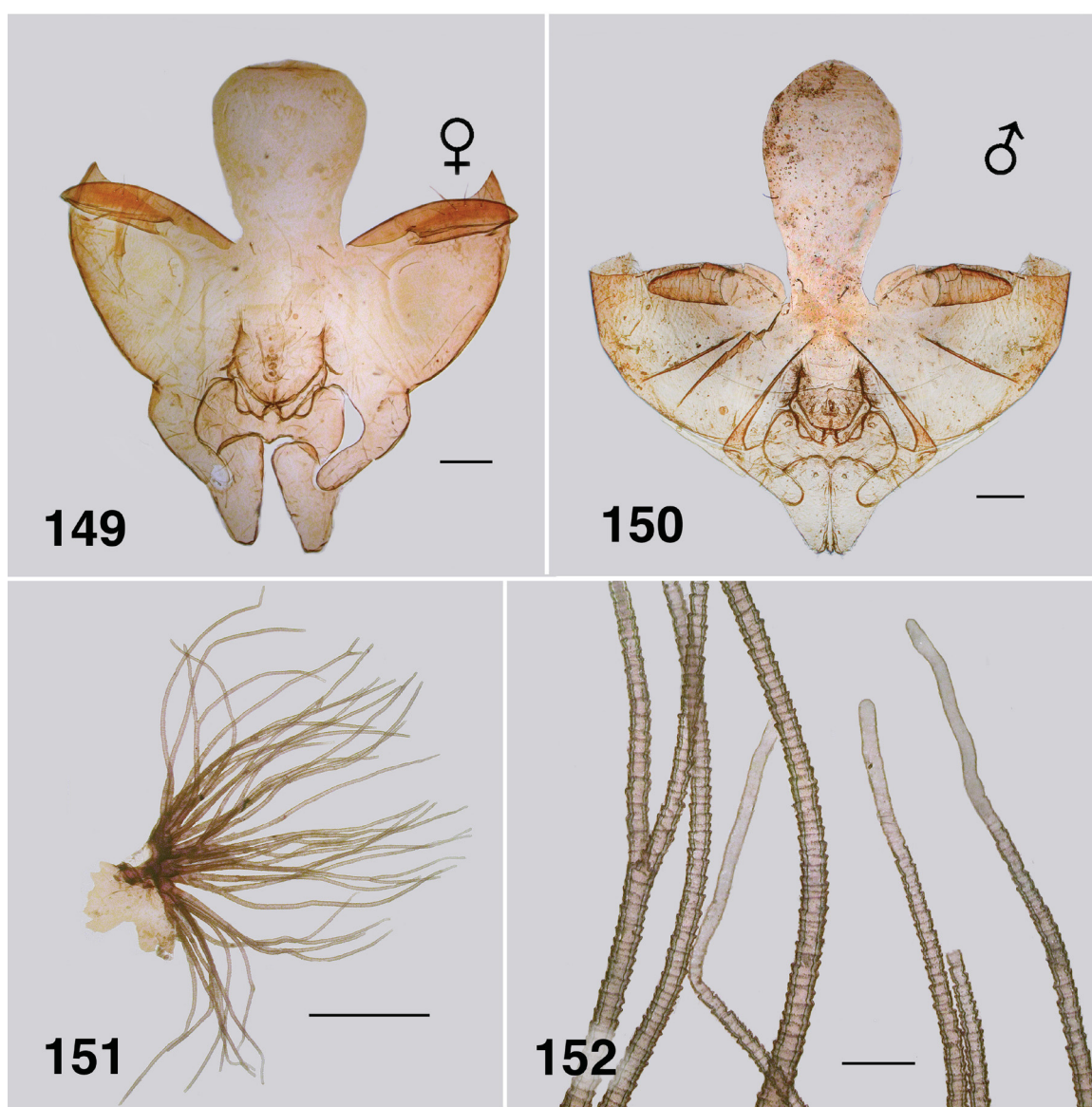
(Fig. 158): variable; not prominent; teeth 0–2 smaller and depressed, flanked by larger tooth 3, number and development per side various; tooth 4 well developed with broad base, protruding; teeth 5–7 small, tooth 8 small, but distinct and directed slightly laterally; ventral edge of hypostoma partially obscuring teeth 0–2; lateral serrations small, numerous and overlapping; four or five short substantial hypostomal setae per side; ratio of hypostoma: genal bridge: postgenal cleft 1.0:1.6:0.5. *Thorax* (Fig. 159): yellowish grey; gill histoblast with five to seven primary trunks visible, occasional bifurcations, directed ventrally, sharply posteriorly then anteroventrally, with filament tips directed anterodorsally, producing overall blunt L-shape. *Prothoracic proleg*: well developed with distinct L-shaped lateral plates; lappets absent, however, some larvae show rudiments of these (e.g., Fig. 50). *Abdomen*: not markedly expanded posteriorly, evenly mottled yellowish brown, paler anteriorly, darker posteriorly. *Rectal papillae*: three simple lobes. *Ventral tubercles*: absent. *Anal sclerite* (Fig. 160): variable, complex, anterior arms flared, occasionally with rectal scales; main body of sclerite moderately developed, posterolateral arms absent; posterior extensions into junction of circlet of hooks not markedly developed, not joined, (i.e., ‘hole’ open); posteroventral arms elongated and finely tapered; ca. five campaniform sensilla (typical number) between the posteroventral arms and circlet of hooks. *Posterior circlet*: not markedly developed, directed posteriorly, ca. 109–119 rows of hooks with 16–19 per row (total ca. 2,000).



FIGURES 144–147. *Austrocnephia orientalis* male. (144) Head, frontal view. (Goomoolahra Falls). Scale bar = 0.25 mm. (145) Genitalia, ventral view. (Little Nerang). Scale bar 0.05 mm. (146) Gonocoxa and gonostylus. (Little Nerang). Scale bar = 0.05 mm. (147) Slide mounted genitalia, showing paramere connector (p c). (Little Nerang). Scale bar = 0.05 mm.



FIGURES 148. *Austrocnephia orientalis* pupa. (148) Female. (Goomoolahra Falls). Scale bar = 1.0 mm.



FIGURES 149–152. *Austrocnephia orientalis* pupa. (149) Female cephalic capsule. Scale bar = 0.1 mm. (150) Male cephalic capsule. Scale bar = 0.2 mm. (151) Pupal gill. Scale bar = 0.5 mm. (152) Gill filament surface. Scale bar = 0.05 mm.

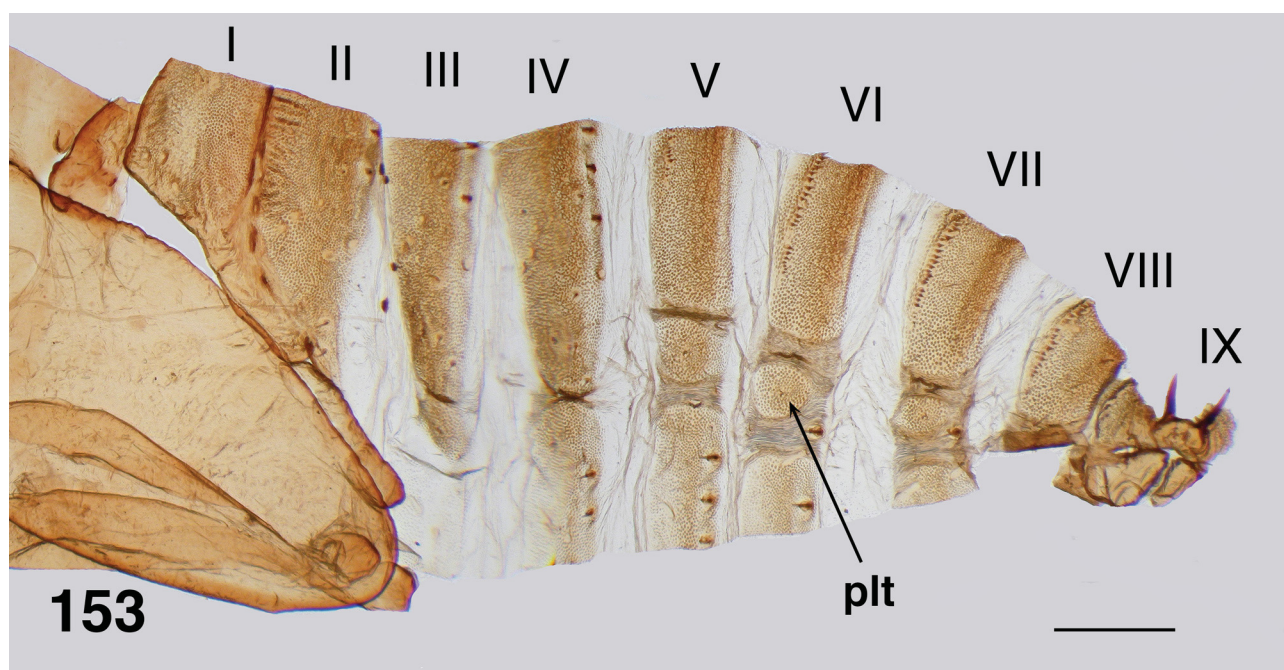


FIGURE 153. *Austrocnephia orientalis* pupa. (153) Abdominal armature. Arrow indicates pleurite (plt). (Goomoolahra Falls). Scale bar = 0.5 mm.

First instar (Three specimens, Purling Brook Falls). *Body*: length, 0.60–0.66 mm. *Head*: length and width 0.13 mm. *Labral fan*: six or seven short rays. *Hypostoma* (Fig. 161): with straight sides, 15 teeth, tooth 0 prominent, teeth 1–3 small, tooth 4 prominent, teeth 5–7 with the first smaller; a single hypostomal seta. *Antenna* (Fig. 162): single article, length 0.023 mm; single apical and two basal sensilla. *Anal sclerite*: not evident. *Posterior circlet*: ca. 50 rows of hooks with three or four hooks per row (total ca. 175).

Pharate 2nd instar larva (from one of the previous 1st instar larvae) (Fig. 162). *Labral fan*: nine or 10 rays. *Hypostoma*: similar in expression to 1st instar; single hypostomal seta. *Antenna*: single article, length 0.036 mm; sensillae as for 1st instar. Other characters not evident.

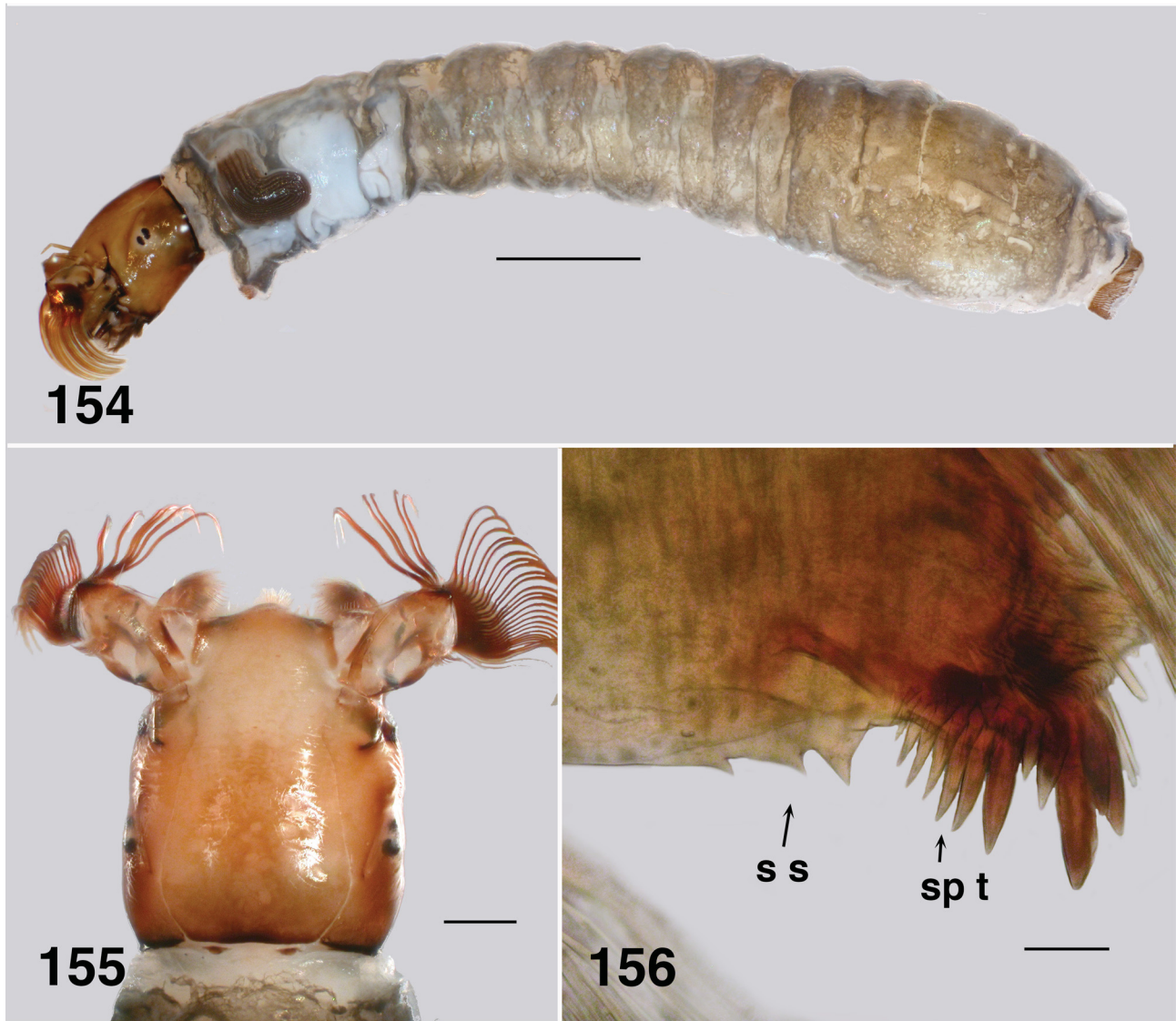
Etymology. Not specified by Mackerras & Mackerras (1950: 170), but clearly named as the eastern form of *Cnephia tonnoiri*.

Types. *Holotype*: Female. Little Nerang Creek, south coast Queensland. September. Coll. Unknown (ANIC). Exact label data not recorded, but probably as for the paratype. Examined by LHG-A in 2007 (Fig. 133).

Paratype: [Little Nerang Cr./S.Q. 10 Aug., 1948] [*Cnephia tonnoiri*/ *orientalis* M.&M./PARATYPE. {F}] [Aust. Nat./Ins. Coll.] Collector not indicated. (S28.1900° E153.2700°). Condition good. Originally on minuten pin, now mounted on slide. A male paratype was photographed by LHG-A in 2007 (Fig. 142). Bugledich (1999: 328) listed two male and one female adult paratypes, plus another male, in the British Museum.

Additional material. Collected mainly by M. Colbo, DAC and JKM. *Alcohol*: Larvae, pupae [ANIC Database No./ 29 026748]; [UASM#/ 370729, 370730; 370801, 370802; 370847, 370848]. *Slide mounts*: All stages [UASM#/ 370782–370800].

Bionomics. Mackerras & Mackerras (1950: 170) state that “*The early stages occur in clear, moderate to fast, turbulent streams, generally adjacent to, rather than in, the line of fastest flow. They are nearly always attached to vegetation, rarely to stones. Adults have not been collected in the field.*” The type locality, Little Nerang Creek (Fig. 163) is shallow with hard rock substrate and fast flow, albeit shallow. Female adults have markedly small mouthparts in relation to head size and reduced numbers of teeth on the lacinia and mandible, plus a well developed claw tooth— indicating ornithophily?



FIGURES 154–156. *Austrocnephia orientalis* larva. (154) Habitus. Last instar. (Hume Highway). Scale bar = 1.0 mm. (155) Dorsal view of head, last instar. (Hume Highway). Scale bar = 0.2 mm. (156) Mandible apex showing serration & sensillum (s s) and spinous teeth (sp t). (Hume Highway). Scale bar = 0.02 mm.

Distribution (Fig. 197). *Queensland*. Mt. Haig, 21 km NEE of Atherton, at light, S17.0900° E145.6000°. 17 Nov. 1981. Adult. Coll. D.H. Colless (ANIC). West of Gordonvale, Goldsborough State Forest, Kearneys Falls, S17.2350° E145.7853°. 24 Mar. 1992. Larvae, pupae. Coll. Zwick. Paluma Range Nat. Park, Little Crystal River, cascade, S19.0156° E146.2641°. 25 April 2002. Larvae. Coll. Zwick (ANIC). Carnarvon Nat. Park, Moss Garden & Hell Hole, S25.0552° E148.2114°. Larva, pupae. Coll. Zwick (ANIC). Carnarvon Nat. Park, Kooraminya Creek, trib. Carnarvon River, S25.0600° E148.2300°, 18 Mar. 1982. Larvae, pupae. Coll. Zwick (ANIC). Carnarvon Gorge, S25.0611° E148.2351°. 4 Nov. 1973. Larvae, pupae. Coll. H.A. Standfast (ROM). Mt. Glorious, Brisbane, Cedar Creek Falls, S27.3220° E152.7762°. 2 May 1974. Larvae, pupae. Coll. D.A. Craig (UASM). Mt. Glorious, Brisbane, S27.3341° E152.7674°. 6 Apr. 1973. Coll. M.H. Colbo (UASM). South Queensland, Upper Mudgeeraba Creek, S28.1630° E153.3100°. 26 Aug. 1950. 10 adults. Coll. Unknown (ANIC). Mudgeeraba Creek, S28.1658° E153.3101°. 26 Aug. 1950, 16 Aug. 1950. Female & males. Coll. Unknown (ANIC). Springbrook National Park, Purling Brook Falls, S28.1898° E153.27091°. 23 June 1971. Larvae. 9 Nov. 1971. Larvae, pupae. Coll. M.H. Colbo (ROM). Purling Brook Falls, S28.1898° E153.27091°. December. Coll. Mackerras (1950). Little Nerang Creek, S28.1906° E153.2710°. 10 Aug. 1948. Female paratype. Coll. Unknown (ANIC). Springbrook South, Purling Brook, S28.1899° E153.2706°. 4 Dec. 1949. Larvae, pupae, adults. Coll. Unknown (ANIC).

South Queensland, Little Nerang River, S28.1890° E153.2710°. Larvae, pupae. Aug. 1948. Coll. Unknown (ANIC). South Queensland, Little Nerang River, S28.1890° E153.2710°. 25 Sept. 1949. Coll. I. & M. Mackerras (ANIC). South Queensland, Little Nerang Creek. S28.1890° E153.2710°. 26 Aug. 1950. Adult. Coll. Unknown (ANIC). Springbrook, S28.1901° E153.2709°. 4 Dec. 1949. Male and females. Coll. Unknown (ANIC). Springbrook National Park, Twin Falls, S28.2000° E153.2700°. 9 Nov. 1973. Larvae, pupae. Coll. M.H. Colbo (ROM). Springbrook, Puky Brook, S28.2100° E153.2700°. 4 Dec. 1949. Larvae, pupae, adults. Coll. Unknown (ANIC). Lamington National Park, S28.2100° E153.1400°. 5 Nov. 1961. Adult. Coll. I.F.B. Common & M.S. Upton (ANIC). South Queensland, Mudgurata Creek, 26 Aug. 1950. Larvae, pupae. Coll. Unknown (ANIC). Springbrook, Blackfellow Creek, S28.4330° E151.4833°. 25 Feb. 1971. Larvae, pupae. Coll. M.H. (ROM). Springbrook, Goomoolahra Falls, S28.2233° E153.2849°. 25 Feb. 1971, 25 Jun. 1971. Larvae, pupae. Coll. M.H. Colbo (ROM). Wilsons Peak, Teviot Brook, S28.2500° E152.4800°. ?-iv-1971. Larvae, pupae. Coll. M.H. Colbo (ROM). Nerang River. 26 Jun. 1971. Larvae. Coll. M.H. Colbo (ROM).

New South Wales. Coutt's Water, near Ebor, S30.3485° E152.4752°. January. Coll. Unknown (Mackerras & Mackerras, 1952). Ebor, Coutts Water, trib., S30.4010° E152.3490°. 10 Jan. 1952. Larvae. Coll. Unknown (ANIC). Macdonald River, Bendemeer, S30.8785° E151.1577°. 30 Sept. 1950. Larva, pupae. Coll. Mackerras (ANIC). Barrington Tops, S32.0660° E151.6620°. March. Coll. McMillan. Laheys Creek, Moonbi Range, S32.2500° E149.3100°. September. Coll. Unknown (ANIC). Hartley, small trib. River Lett, S33.5400° E1700°. 12 Oct. 1950. Larvae. Coll. Unknown (ANIC). Hartley, S33.5440° E1705°. 9 Dec. 1931. 7 adults. Coll. F.H. Taylor (ANIC). Orange, Mt. Canoblas, Molong Creek, S33.3350° E149.0190°. 10 Oct. 1958. Larvae. Coll. Unknown (ANIC). Mt. Canoblas, Molong Creek, S33.3350° E149.0190°. 12-15 Oct. 1950. two reared adults. Coll. Unknown (ANIC). Brown Mt., Rutherford Creek, S36.5920° E149.4450°. 17 Jul. 1963. Adult. Coll. Z. Liepa (ANIC). Janolan Caves, S33.8190° E150.0220°. No date. Adult. Coll. J.C. Wiburd (ANIC). Bendemeer, Macdonald River, S30.8920° E151.1570°. 3-6 Oct. 1950. two reared adults. Coll. Unknown (ANIC). Several creeks between Mt. Canoblas and Bumbery, Orange District, S33.3000° E149.0600°. October. Coll. Unknown (ANIC). Hartley, Lett River, S33.5400° E150.1700°. October. Coll. Unknown (ANIC). Jenolan Caves, S33.8200° E150.0500°. Male. Coll. J.C. Wilburo (ANIC). Alpine Highway, Tom Groggin, Murray Gorge, Snowy Creek, S36.5377° E148.1348°. 16 Nov. 2011. Larvae. Colls. D.A. & R.E.G. Craig (UASM).

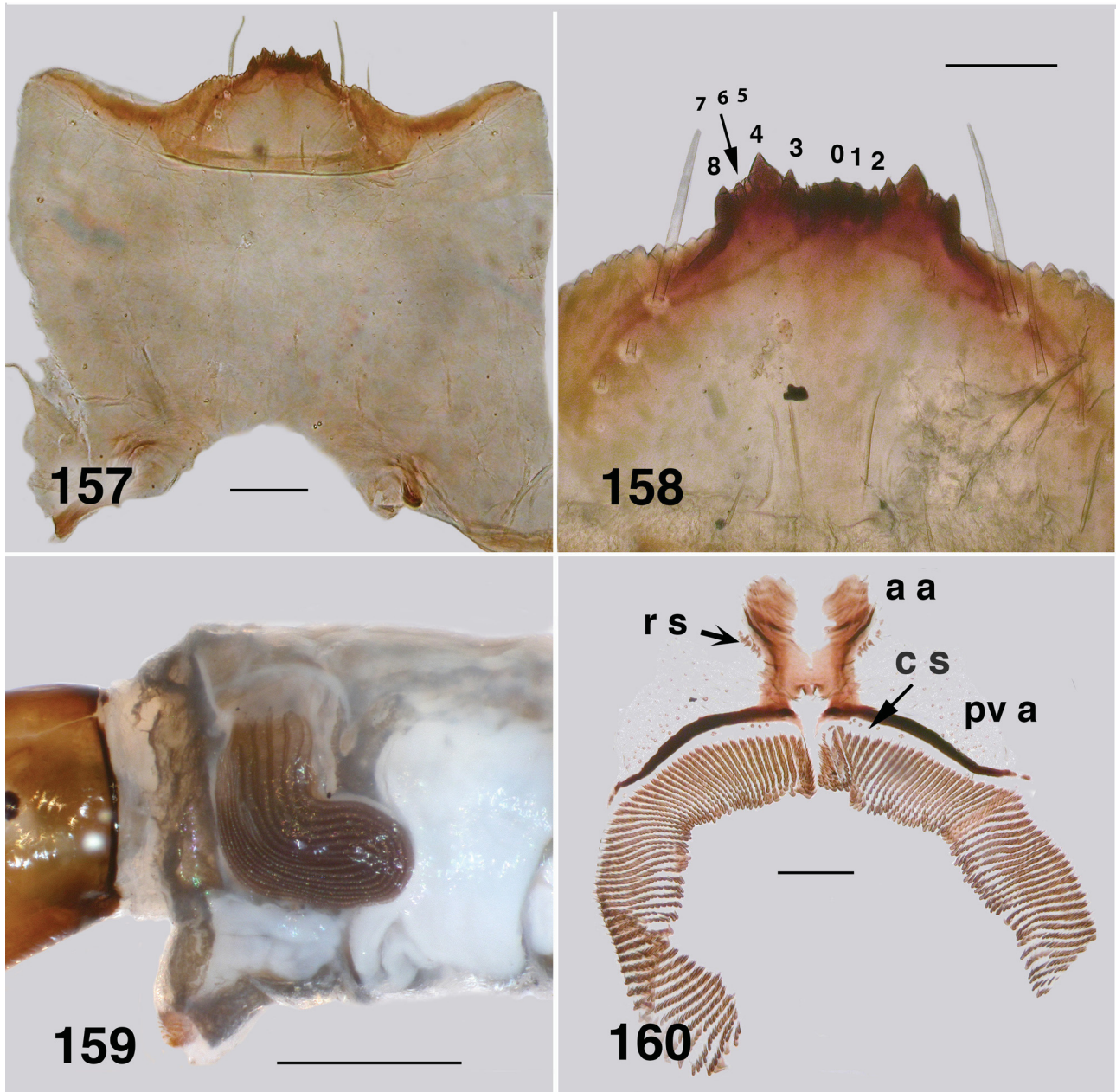
Australian Capital Territory. Upper Paddy's River, S35.4600° E149.0200°. 9 Sept. 1962. Larvae. Coll. Unknown. Det. J. Prince (ANIC). Upper Paddy's River, S35.4600° E149.0200°. 17 Nov. 1962. Adult. Coll. Unknown (ANIC). Paddy's River, near Cotter Junction, S35.3264 E145.9480. 16 Nov. 1949. Larvae. Coll. Unknown (ANIC). Coree Creek, S35.3300° E148.8700°. 25 Jan. 1931. Adult. Coll. A.L. Tonnoir (ANIC). Canberra, S35.2740° E149.1140°. 6 Nov. 1929. Adult. Coll. A.L. Tonnoir (ANIC). Black Mountain, CSIRO. Light trap, S35.2740° E149.1140°. Adults. 10 Aug. 1953. Coll. A. Dyce, 23 Oct. 1959, 9 June 1961. Coll. I. F. B. Common, Black Mountain, Light trap on CSIRO, S35.2748° E149.1134°. 23 Oct. 1959. Female. Coll. I.F.B. Common (ANIC). Canberra, S35.2823° E149.1287°. November (Tonnoir) (Mackerras & Mackerras, 1952, 1955). Cotter River, S35.3200° E148.940°. Nov. (Mackerras & Mackerras). Uniarra State Forest, Coree Creek, S35.3300° E148.8700°. Nov, Jan. (Tonnoir), (Mackerras & Mackerras). Paddy's River, S35.4500° E149.0500°. Nov. (Mackerras). Tidbinbilla Nature Reserve, trib Tidbinbilla River, Lyrebird Stream S35.4559° E148.8830°. 18 Sept. 2011. Pupa. Colls. D.A. & R.E.G. Craig (UASM). Pierce Creek Forest, Scenic Road, culvert, 1.7 km from Paddys Road, S35.3498° E148.9491°. 24 Sept. 2011. Larvae. Colls. D.A. & R.E.G. Craig (UASM).

Victoria. Log bridge Creek, West Corryong, S36.2100° E147.7100°. 16 Sept. 2006. Larvae. Coll. Zwick. Snobs Creek Falls, S37.3300° E145.8990°. 19 Dec. 1972 Larvae. Coll. Zwick (ANIC).

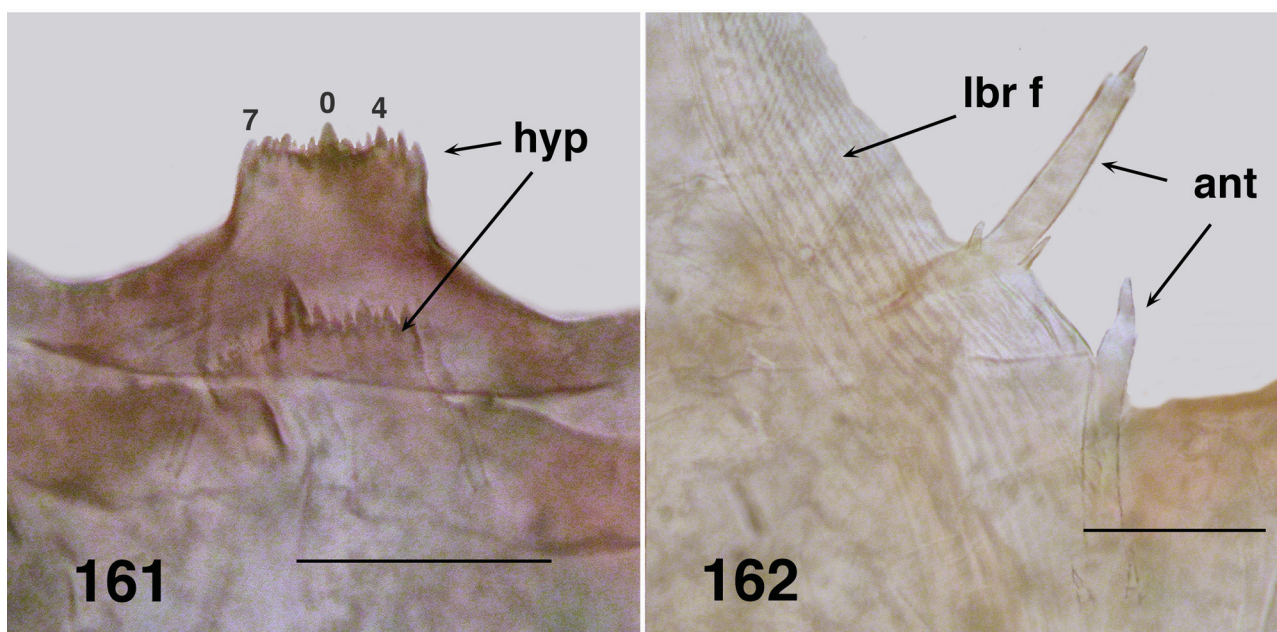
South Australia (Adelaide Peninsula). Scotts Bottom, S34.9691° E138.9445°. Sept. Brownhill Creek, S34.9896° E138.6373°. Sept. Sellicks Hill, S35.3300° E138.4800°. Oct. Myponga Creek, S35.3760° E138.4980°. Sept. Coll. Lines. (Mackerras & Mackerras, 1955).

Tasmania. Cam River, Back Cam Road, S41.0432° E145.0172°. CAMR01. 22 Aug. 2006. Larvae. Coll. M. Jack. DPIPWE (TMAG). Rheban, Sandspit River, S42.6460° E147.8990°. 21 Jan. 1949. Larvae, pupae. Coll. Unknown (ANIC). Pyengana, S41.2800° E148.000°. 2 Mar. 1963. Adult. Coll. I. F. B. Common & M. S. Upton (ANIC). Penguin, Penguin Creek, Hayward Street, S41.1140° E146.0689°, BLYT04. 18 Nov. 2005. Larvae. Coll. D. Horner, DPIPWE (TMAG). Don River, Sheffield Road, S41.2829° E146.3189°, MERS37. 18 Oct. 2006. Larvae. Coll. T. Krasnicki, DPIPWE (TMAG). Arthur River, Pykes Bridge, S41.2936° E147.4160°, ARTH01. 21 Mar. 2007. Larvae. Coll. T. Krasnicki DPIPWE (TMAG). Emu River, Fern Glade Reserve, S41.2981° E147.9572°, EMUR01, 5

May 2005. Larvae. Coll. D. Horner, DPIPWE (TMAG). Florentine River, Florentine Road, S41.4947° E146.8171°, UDER008. 22 Mar. 2005. Larvae. Coll. T. Krasnicki, DPIPWE (TMAG). North West Bay River, Miandetta Drive, S42.0084° E147.2503°, HOBA04. 12 Oct. 2005. Larvae. Coll. D. Horner DPIPWE (TMAG). Rheban, Griffith River, Sandspit River, S42.6460° E147.8996°. January. Coll. Mackerras. (Mackerras & Mackerras, 1950: 170). North West Bay River, Huon Highway, S42.9705° E147.1973°, HOBA07. 4 Oct. 2005. Larvae. Coll. S. Meyer, DPIPWE (TMAG). Allens Rivulet, Sandfly Road, S42.9914° E147.2070°, HOBA13. 13 Oct. 2005. Larvae. Coll. J. Latton, DPIPWE (TMAG). North West Bay River, Margate weir, S42.9923° E147.2246°, HOBA05. 12 Oct. 2005. Larvae. Coll. T. Krasnicki, DPIPWE (TMAG). North West Bay River, upstream of Allens Rivulet, S42.9939° E147.2245°, HOBA06. 20 Apr. 2006. Larvae. Coll. T. Krasnicki, DPIPWE (TMAG). Mountain River, Ranelagh Bridge, S43.0138° E147.0495°, HUON018. 27 Sept. 2005. Larvae. Coll. S. Meyer, DPIPWE (TMAG). North West Bay River, Channel Highway, S43.0213° E147.2655°, HOBA01. 5 Oct. 2005. Larvae. Coll. T. Krasnicki, DPIPWE. TMAG.



FIGURES 157–160. *Austrocnephia orientalis* larva. (157) Ventral head cuticle. (Hume Highway). Scale bar = 0.1 mm. (158) Hypostoma. (Hume Highway). Scale bar = 0.05 mm. (159) Pupal gill histoblast. (Hume Highway). Scale bar = 0.5 mm. (160) Anal sclerite showing anterior arms (a a), campaniform sensilla (c s), posteroventral arms (pv a), rectal scales (r s) and circlet of hooks. (Mt. Glorious). Scale bar = 0.1 mm.



FIGURES 161, 162. *Austrocnephia orientalis* larva. (161) First and pharate second instar larval hypostoma (hyp). (Purling Brook). Scale bar = 0.02 mm. (162) First and pharate second instar larval antennae (ant) and labral fan (lbr f). (Purling Brook). Scale bar = 0.02 mm.

Remarks. The distribution of *A. orientalis* is of some interest. It is widespread in Queensland, New South Wales, Australian Capital Territory and Tasmania, however, not so in Victoria where it is known only from two localities and in South Australia only from the Adelaide Peninsula. Given the intense collecting by the authors in Victoria this gap would appear to be correct. Further collection from the Adelaide Peninsula might be informative.

Mackerras & Mackerras (1950: 170) noted that it was not possible to distinguish the female adults of the then *orientalis fuscoflava* from those of *fuscoflava* and that it was closely related to *aurantiaca* and *tonnoiri*, albeit *aurantiaca* lacked the spot on the wing. They comment on differences in number of gill filaments—the type locality and southern populations having lower numbers—50. Further, those with higher numbers had filaments branching close to the base. Our observations agree in that those with lower numbers do not. Colbo (pers. com., 2012) also knows of populations from Carnarvon Gorge (500+ km NW of Brisbane, S25.0500° E148.2200°) that have much larger numbers of gill filaments. These discrepancies are indicative of closely related entities, similar to that hypothesized for *A. aurantiaca*. Indeed, material from Springbrook has larvae where the anal sclerite is similar to that of *aurantiaca*, but the overall head is as for *orientalis*, however, the maxilla and mandible are *aurantiaca*-like, while the pupa has abdominal pleurites, as does *orientalis s.s.*

Craig (1974) and Ross & Craig (1978) reconfirmed that 1st instar larvae of Prosimulini virtually lack labral fans; apparently first noted by Strickland (1913: 48) and definitively so by Davies (1960: 81). Colbo (1974: His Fig. 4) illustrated the 1st instar larval head structures of *A. orientalis*, clearly showing distinct labral fans and we have observed these as well. Similarly for *A. tonnoiri* (Fig. 193); supporting well the contention that *Austrocnephia* is not Prosimulini. Colbo (*loc. cit.*) also illustrated a minute anal sclerite for *A. orientalis*. For *A. tonnoiri* 1st instar larvae (see latter) there is but a faint trace of this sclerite. This is of interest since Crosby (1974: 23) indicated the anal sclerite was absent in *Austrosimulium* 1st instar larvae, developing only in the 2nd.

Other characters of interest in mature larvae are the markedly serrated lateral edges of the hypostoma (Fig. 158) and apparent ‘rectal scales’ on either side of the anal sclerite anterior arms (Fig. 160), unique within the genus. Colbo (1974: 66) noted those as well. Further, while the central gap of the anal sclerite has medial posterior projections as seen in the *aurantiaca* species-group, the number of campaniform sensilla between the posteroventral arm and the circlet of hooks is four to five—more typical for simuliids.

***Austrocnephia tonnoiri* (Drummond 1931). New combination.**

(Figs. 164–195)

Simulium tonnoiri Drummond 1931: 6; original designation.

Cnephia tonnoiri tonnoiri. Mackerras & Mackerras, 1950: 169; new combination.

Cnephia tonnoiri. Rothfels, 1979: 522.

(‘*Cnephia*’ of authors) *tonnoiri*. Crosskey, 1987: 443; undetermined genus in Prosimuliini.

(Unplaced species of Prosimuliini) *tonnoiri*. Crosskey, 1989: 222.

Cnephia tonnoiri tonnoiri. Trayler *et al.*, 1996: 286.

Paracnephia tonnoiri. Crosskey & Howard, 1997: 18; new combination, unplaced to subgenus. Bugledich, 1999: 328. Crosskey & Howard, 2004: 10. Adler & Crosskey, 2008: 26; transferred to Simuliini, unplaced to subgenus. Adler, 2019: 33.

Redescription. *Adult female* (based on a few pinned adults plus pharate adults and literature description). *Body*: head and thorax brownish orange (Figs. 164, 165); abdomen yellow and black; total length *ca.* 2.8–2.9 mm. *Head* (Fig. 166): overall reddish brown; width 0.85–0.97 mm, depth 0.57–0.63 mm; postocciput black, vestiture of dense hairs; frons not markedly narrowed, dark brown, vestiture of moderately dense silvery hairs; frons:head-width ratio 1.0:0.6:0–6.2. *Eyes*: interocular distance 0.16 mm; dark blackish orange, upper ommatidia lighter; ommatidia diameter 0.023 mm; *ca.* 37 rows across and down at mid-eye. *Clypeus*: width 0.18–0.24 mm; dark brown, moderate vestiture of fine silvery hairs. *Antenna*: total length 0.73–0.78 mm, extended well beyond posterior margin of head; evenly dark brown; scape and pedicel slightly broader than flagellomere I, flagellomere II shorter than first, remainder rectangular, barely tapered to apex. *Mouthparts*: moderately developed, *ca.* 0.4× length of head depth; maxillary palp, total length 7.4 mm, palpomeres I & II small, palpomere III darker brown than others, dense vestiture, IV small, V elongated; proportional lengths palpomeres II–V 1.0:0.7:1.5; sensory organ moderately elongated, 0.65× length of palpomere III, opening normal; mandible pointed apically with *ca.* 27 markedly small inner teeth, outer teeth absent, but with irregular edge, essentially as for *A. fuscoflava*; lacinia with 13–15 teeth on inner edge, nine teeth on outer; cibarium (Fig. 167) cornuae broad basally, not markedly flared, tapered and curved apically, medial gap small and angulate. *Thorax*: length 1.4 mm, width 1.3 mm; evenly orange brown; postpronotal lobe well developed with dense fine hair, scutellum slightly paler than scutum, vestiture of sparse very fine yellowish hairs, long black hairs laterally; postnotum concolourous with scutellum; antepronotal lobe with dense pale hair; proepisternum and fore coxa bare; pleuron light brown, anepisternal membrane bare; katepisternal sulcus shallow and broad. *Wing*: length 2.8–3.4 mm, width 1.5–1.7 mm; membrane slightly fumose on apex and anal lobe, area between costal and radial sector veins faintly yellowish; distal 2/3 of costa with spines, distal 1/3 Sc bare, Rs not branched; a:b ratio 1.0:2.7; M_1 appearing distinctly doubled; CuA slightly sinuous; markedly distinct small pigmented region at r-m cross veins—comprised of pigmented sclerotized region, pigmented veins and concentration of hairs (as for male, *i.e.*, Fig. 176). *Haltere*: stem pale, knob darker. *Legs*: evenly yellowish brown, joints tending to darker; hind basitarsus with regular row of stout spines, absent distally; calcipala markedly developed with dorsal notch; pedisulcus only moderately expressed; tarsomere II *ca.* 1.8× as long as distal width; claw talon fine (Fig. 168) and smoothly tapered, basal tooth cone-shaped, 1/3 length of talon, rounded heel moderately expressed. *Abdomen*: basal scale dark brown, vestiture of long yellowish hairs; anterior segments yellowish, other segments dark brown, vestiture of dense long pale hairs laterally and posteriorly; tergites markedly poorly sclerotized, barely discernable from remainder of dorsum. *Genitalia*: sternite VIII dark with distinct anterior edges and medial region, vestiture of microtrichia, large strong hairs posterolaterally; hypogynial valves (Fig. 169) lightly pigmented, vestiture of triads of microtrichia and strong hairs apically, medial edges of valves slightly concave, lightly strengthened anteromedially, moderately rounded apically, with ill-defined edge; cercus in lateral view elongated and rounded apically, with slight medial depression, anal lobe elongated, subequal in length to cercus (Fig. 170); genital fork (Fig. 171) finely expressed, anterior stem narrow, rounded apically, when in situ markedly curved dorsally (distorted in image), no indication of membranous lateral areas, lateral arms narrow, apodeme absent, lateral plates bifurcate; spermatheca elongate and ovoid, dark brown, slightly wrinkled, internal fine spines not obvious, clear membranous area at junction with spermathecal duct small with raised edge (Fig. 172).

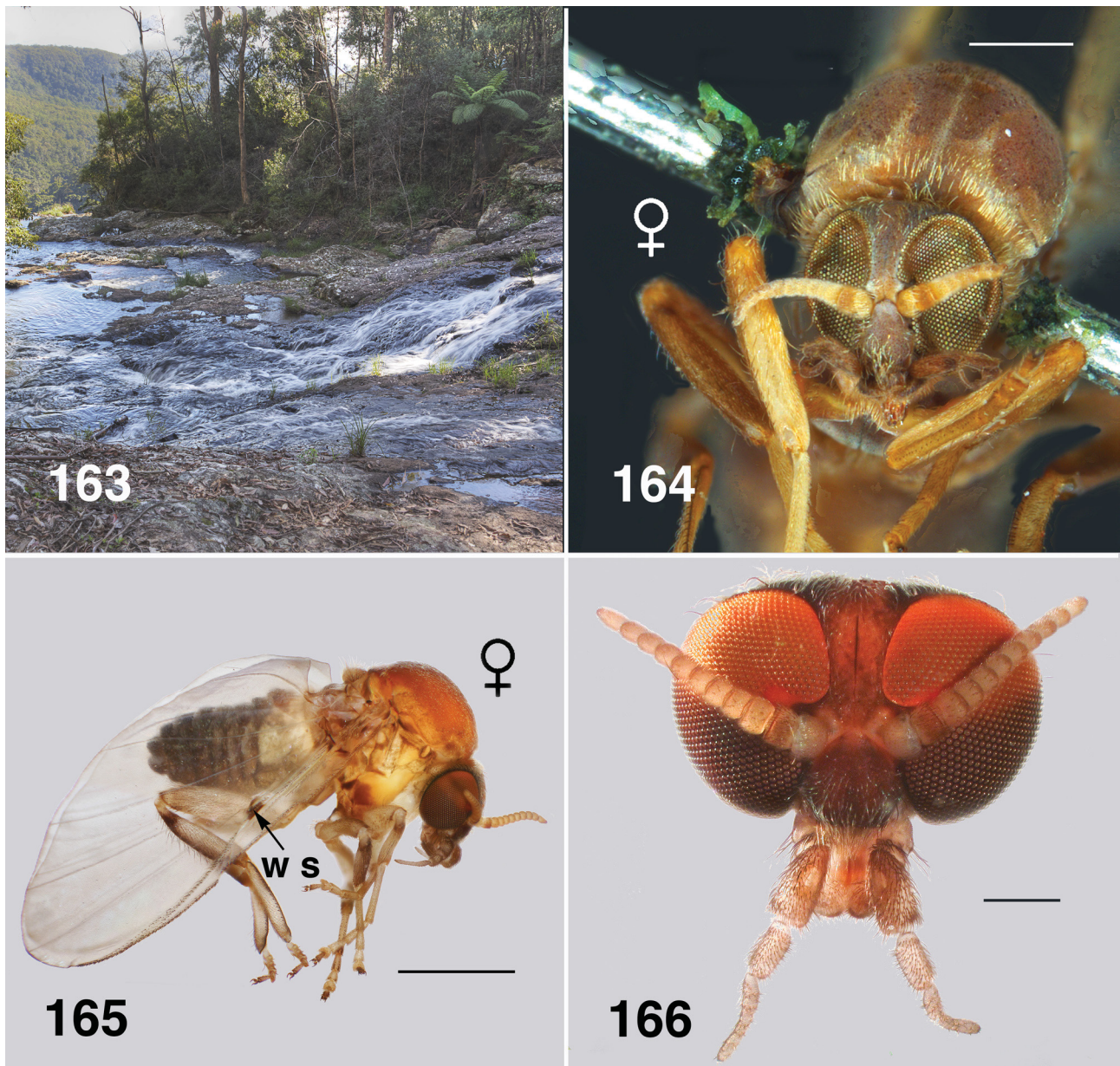
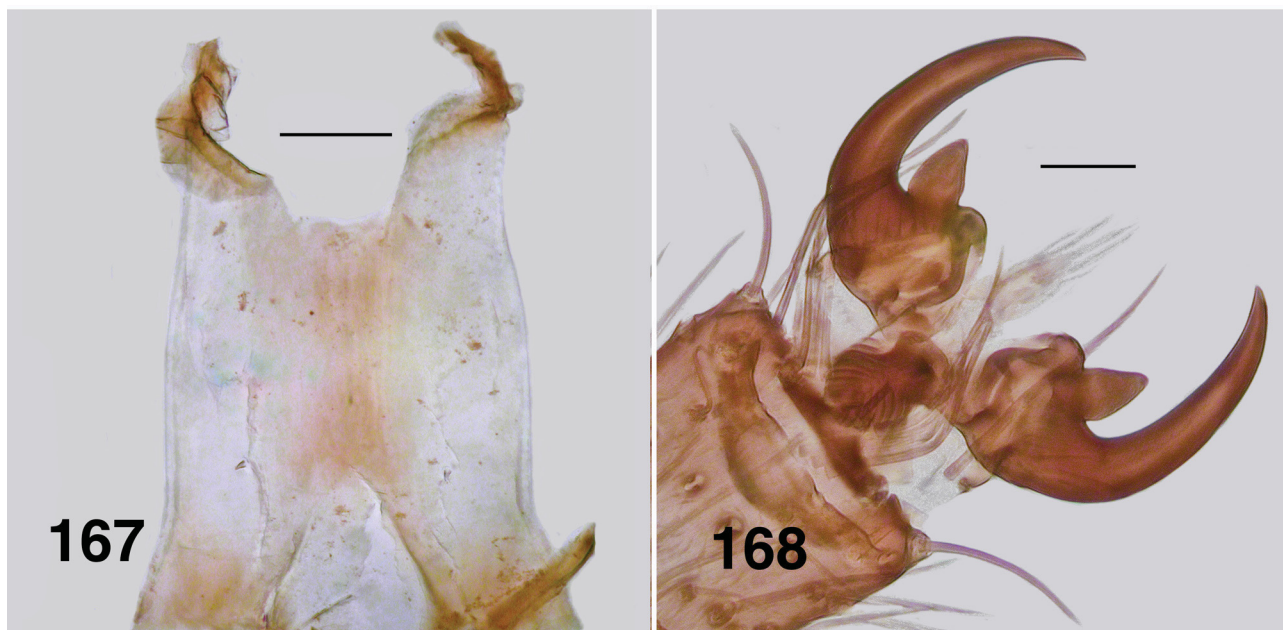


FIGURE 163. *Austrocnephia orientalis*. (163) Type locality, Little Nerang Creek. Queensland, April 2013. Image courtesy of Alan Moore & FreeLargePhotos.com. **FIGURES 164–166.** *Austrocnephia tonnoiri* female. (164) Frontal view. (Little Nerang Creek). Image by LHG-A. Scale = bar 0.5 mm. (165) Habitus of *A. tonnoiri* female. (Kangaroo Gulley). Arrow indicates wing spot (w s). Scale bar = 1.0 mm. (166) Frontal view of head. (Stony Brook). Scale bar = 0.2 mm.

Adult male (lectotypes and other specimens from ANIC). *Body* (Figs. 173, 174): overall yellowish orange and black; total length 2.3–3.1 mm. *Head* (Fig. 175): overall brown; width 0.90–0.95 mm, depth 0.71–0.79 mm; hairs yellow. *Eyes*: upper ommatidia bright yellowish orange, large, diameter 0.047 mm, *ca.* 16 across and down; lower ommatidia blackish orange, markedly smaller, diameter 0.018 mm, *ca.* 32 across and down. *Clypeus*: black; width 0.13–0.21 mm; vestiture of sparse stiff black hairs. *Antenna*: total length 0.57–0.75 mm; darker basally, evenly yellowish brown otherwise; scape and pedicel subequal in length, scape dark brown, flagellomere I slightly narrower than scape, other flagellomeres tapered slightly to apex. *Mouthparts*: insubstantial; length 0.16–0.20× head depth; maxillary palp 0.63 mm long, palpomeres I & II small, palpomeres III & IV subequal in length, proportional lengths of palpomeres III–V 1.0:0.8:1.8, sensory vesicle spherical in shape, occupying 0.25× palpomere length, opening 0.5× vesicle width; lacinia with hairs apically; mandible not observed. *Thorax*: length 1.3–1.4 mm, width 0.80–0.96 mm; markedly domed, head angled ventrally; postpronotal lobe with slightly longer hairs than scutum; anteprenotal lobes with sparse clump of longish fine pale hairs, scutum evenly medium brown, vestiture of fine golden hairs

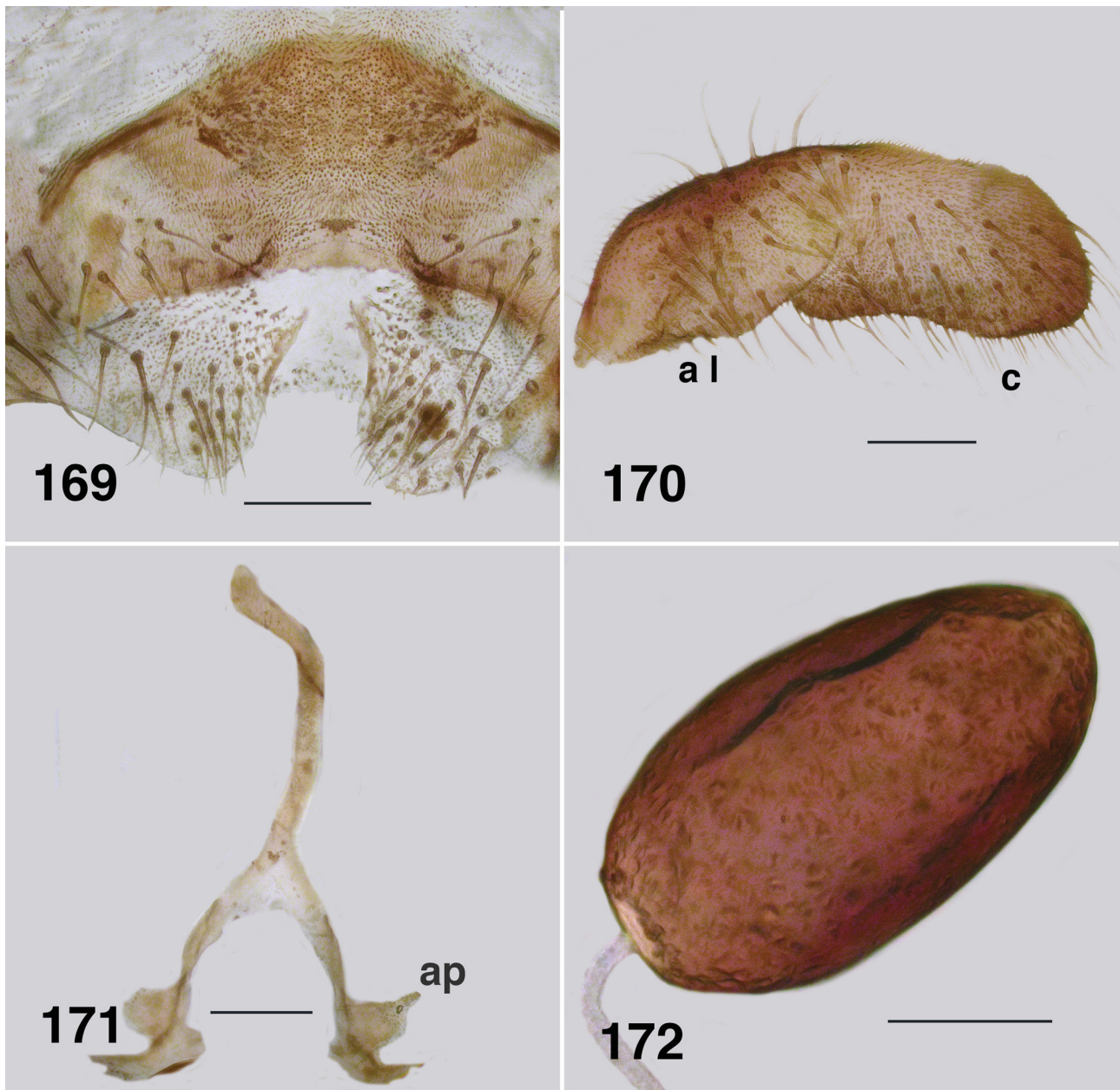
longer anteriorly, scutellum concolourous with scutum, vestiture of long pale hairs laterally, postnotum darker than scutum; proepisternum bare; pleuron brown, anepisternal membrane bare. *Wing*: length 2.9 mm, width 1.4 mm; membrane slightly fumose at apex, slightly so on anal lobe; yellowish tint between C and Sc; basal medial cell not apparent; a:b ratio 1.0:3.0; costa with spines, marked pigmented region at r-m cross veins, comprised of concentration of hairs on R_1 and pigmentation of junction (Fig. 176); R_s not branched; M_1 appearing distinctly doubled, CuA not markedly sinuous. *Haltere*: base of stem pale, knob dark tan. *Legs*: overall yellowish with dark articulations; hind basitarsus with ventral row of stout spines, absent distally; calcipala essentially as for female; tarsal claw as for other species. *Abdomen*: overall yellow and black, basal scale hairs pale yellow, extended to posterior of segment IV, tergites not markedly sclerotized, 2.0–3.5× as wide as long, markedly hirsute laterally, more so on posterior segments, hairs yellowish, long and dense; pleurites absent; sternites essentially absent, slightly expressed posteriorly. *Genitalia*: overall small and moderately sclerotized (Fig. 177); gonocoxa 2× longer than its basal width, strengthened and scalloped posteromedially, vestiture of sparse hairs (Fig. 178); gonostylus in ventral view narrowed and tapered, broad in lateral view, approximately 1.5× longer than basal width, two substantial, short, blunt, apical spines; ventral plate (Fig. 179) small, simple, 2.0× wider than long in ventral view, posterior edge thickened apically, slightly concave to convex (depending on view), broadly rounded laterally with straight edge angled anteriorly towards basal arms, slightly convex anteromedially, vestiture essentially absent, but with sparse central hairs, basal arms distinct, albeit not markedly developed, paramere connectors well expressed; median sclerite poorly expressed, as two widely separated arms extended just beyond posterior edge of ventral plate, junction with ventral plate not obvious; parameres plate-like basally, tapered distally with corrugations apically, spines poorly expressed as three or four small blunt structures (Fig. 178); adeagal membrane with sparse microtrichia.



FIGURES 167, 168. *Austrocnephia tonnoiri* female. (167) Cibarium. Paratype. Scale bar = 0.05 mm. (168) Tarsal claws. (Serpentine). Scale bar = 0.02 mm.

Pupa (based on numerous specimens). *Body*: female length 3.0–4.2 mm (Fig 183), male length 3.2–3.6 mm; cuticle clear brown. *Head*: frons of female quadratic, ratio of basal width to vertex width and height, 1.0:1.3 and 1.0:1.6 respectively (Fig. 180), that of male ovoid; ratios 1.0:1.9 and 1.0:2.5 respectively (Fig. 181), cuticle not tuberculate; in male, frontal and facial setae present, in female frontal setae absent, in both male and female facial setae are well developed and curved—almost spine-like; antennal sheath of female extended beyond margin of ocular shield, that of male markedly not so. *Thorax*: smooth, dorsocentral setae, stiff, spine-like, tips usually curled. *Gill* (Fig. 182): total length ca. 0.95–1.60 mm; antler-like with 26–36 filaments arising from five to seven markedly short basal trunks, branching at irregular intervals, some branches short, surface with distinct fine pseudoannulations, smooth apically; tips often broken in mature pupae, otherwise as for *A. orientalis*. *Abdomen* (Fig. 184): essentially as for *A. fuscoflava*.

Cocoon (Fig. 183). Close fitting, usually covering pupa completely, slightly slipper-shaped; irregular weave, silk fibers fine; considerable extraneous material incorporated.



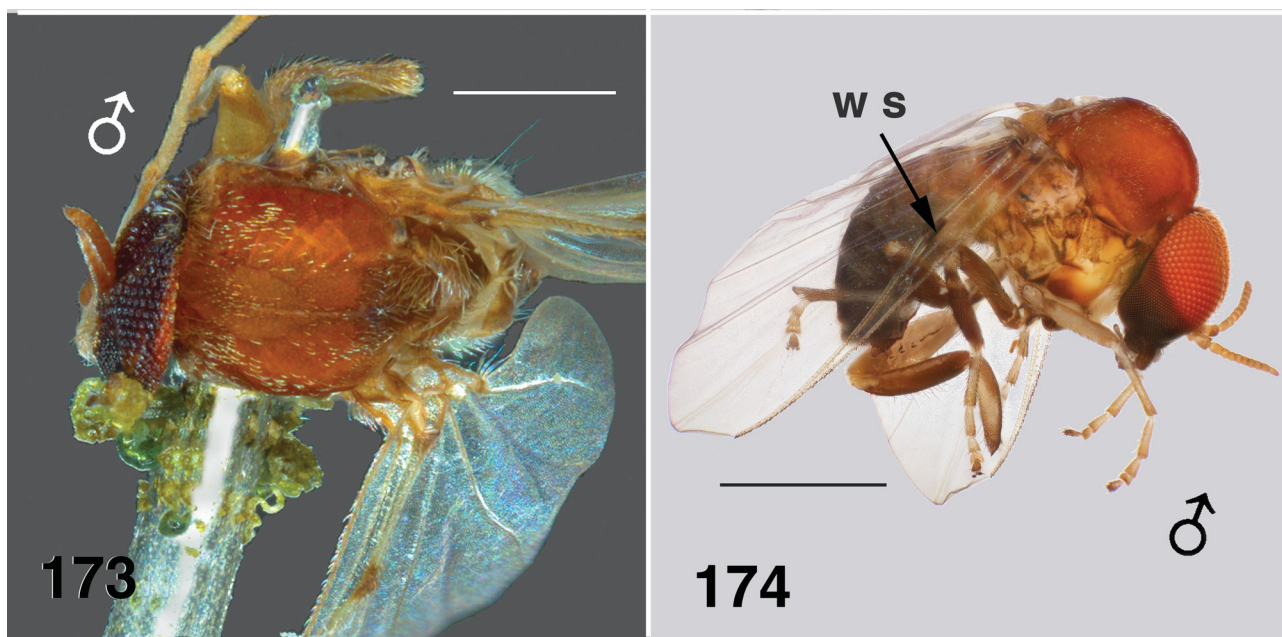
FIGURES 169–172. *Austrocnephia tonnoiri* female. (169) Hypogynial valves. Paralectotype. (Lesmurdie). Scale bar = 0.05 mm. (170) Anal lobe (a l) and cercus (c). Paralectotype. Scale bar = 0.05 mm. (171) Genital fork, showing apodeme (ap). Paralectotype. Scale bar = 0.05 mm. (172) Spermatheca. (Serpentine). Scale bar = 0.05 mm.

Larva (based on numerous specimens, Kangaroo Gully). *Body* (Fig. 185): total length 6.6–7.6 mm; overall mottled grey; smoothly expanded from the thorax posteriorly. *Head* (Fig. 186): overall markedly bicolourous, yellow and dark brown, head spot pattern positive; length 0.75–0.96 mm, width 0.71–0.83 mm; distance between antennal bases 0.36–0.43 mm; anterior margins of head subparallel, diverging posterior of stemmata; ecdysial lines well visible, slightly divergent until posterior of stemmata, then very broadly curved laterally then medially; cervical sclerites elongated and fused to postociput; genae brown. *Antenna*: not extended to end of labral fan stem; total length 0.30–0.35 mm; basal article pale proximally, darker brown distally, medial article and distal articles evenly light brown; medial article slightly narrowed along length, basal article markedly shorter than medial article, proportional lengths of basal, medial and apical articles 1.0:1.2:1.7. *Labral fan*: stem short, not markedly pigmented, ca. 26–36 fine rays, ten posterior rays finer than others, length 0.74–0.88 mm, mid-ray width 0.014–0.018 mm; pattern of microtrichia not marked, longer microtrichia subequal in length to ray width. *Mandible* (Fig. 187): darkly pigmented; not noticeably short; outer teeth short and distinct; apical tooth prominent; subapical teeth small and

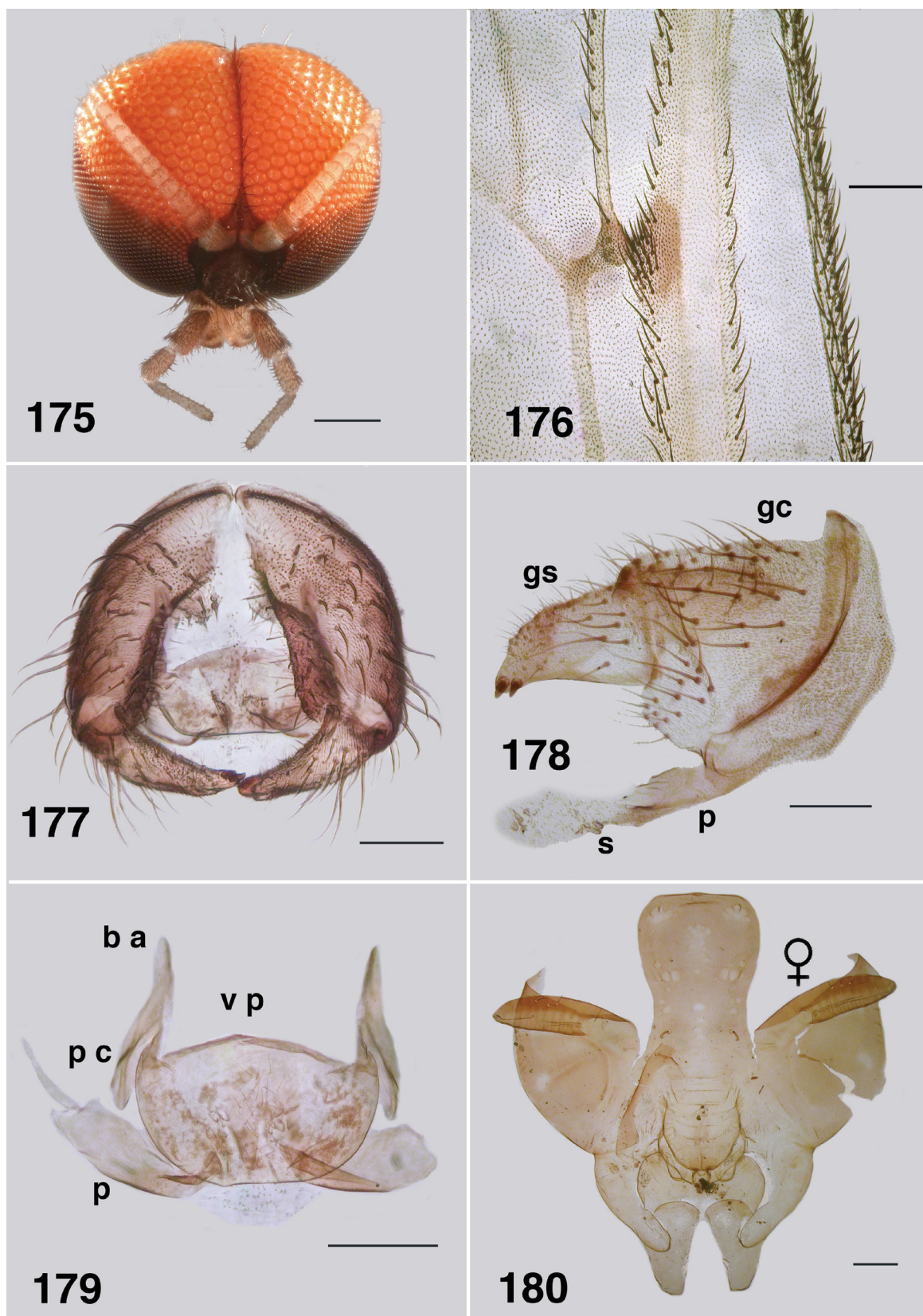
subequal in length; *ca.* six spinous teeth, distal tooth markedly developed, others short; serration and sensilla well developed, slightly complex; blade region short and straight. *Maxilla*: palp cone-shaped 2.4–2.6× as long as basal width, very dark; hairs at base of palp not markedly developed, various. *Postgenal cleft* (Fig. 188): markedly shallow with medial projection—variable; posterior tentorial pits distinct and rounded; postgenal bridge evenly pale contrasting with slightly darker genae; elongated posteroventral muscles spots distinct, but not markedly so; suboesophageal ganglion slightly pigmented and obvious. *Hypostoma* (Fig. 189): well pigmented; tooth 0 distinct but not markedly prominent, teeth 1 & 2, small, tooth 3 larger (various, often absent from one side), tooth 4 well developed and flanged; teeth 5–7 small and various, tooth 8 small, obvious, and directed slightly laterally; ventral edge of hypostoma partially obscuring teeth 5–7; lateral edges of hypostoma straight, six to nine small lateral serrations, other smaller serrations more laterally; four or five substantial hypostomal setae on each side; ratio of hypostoma to genal bridge and postgenal cleft 1.0:1.3:0.3. *Thorax*: mottled grey; gill histoblast (Fig. 190) broadly L-shaped, with five primary trunks visible, directed ventrally, then posteriorly, then sharply anteroventrally; thinner pale tips of filaments directed anterodorsally. *Prothoracic proleg* (Fig. 191): lateral plates not markedly developed or L-shaped; lappets sometimes present as small clear tubercles. *Abdomen*: evenly expanded from anterior to posterior segments, not markedly expanded at segments VII & VIII; evenly mottled medium grey, paler anteriorly, darker posteriorly with some yellow. *Rectal papillae*: three simple lobes. *Ventral tubercles*: absent. *Anal sclerite* (Fig. 192): anterior arms slightly flared; main body of sclerite not well developed; posteromedial hole open, posterolateral arms absent; posteromedial extensions projecting from base of each posteroventral arm into the dorsal junction of hooks in circlet not markedly developed; posteroventral arms elongated and finely tapered; only five to eight campaniform sensilla between the posteroventral arms and circlet of hooks. *Posterior circlet*: well developed, *ca.* 150 rows of hooks with 17–23 hooks per row (total *ca.* 3,100).

First instar (one specimen). *Body*. Length 0.79 mm; head (Fig. 193). *Labral fans*: *ca.* 12 fan rays, length *ca.* 0.08 mm. *Hypostoma* (Fig. 194): tooth 0 prominent, teeth 1–3 subequal, tooth 4 slightly larger, teeth 5 & 6 present, teeth 7 & 8 barely evident; hypostomal groove distinct. *Anal sclerite*: barely evident, associated campaniform sensilla distinct. *Circlet of hooks*: with *ca.* 45 rows of hooks, with two or three hooks per row (total *ca.* 112).

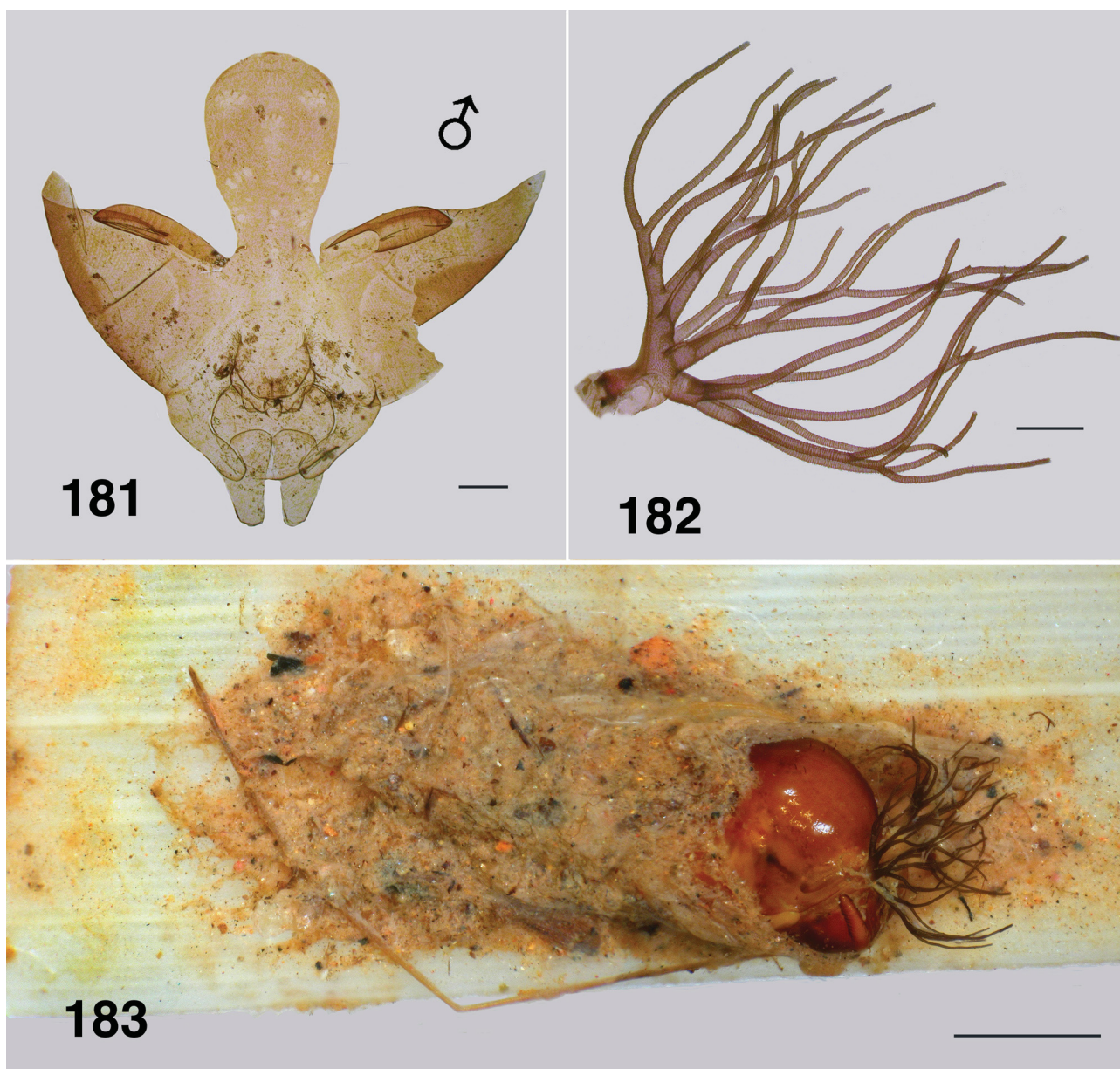
Etymology. Named by Drummond (1931: 6) in honour of Australasian simuliidologist André Léon Tonnoir.



FIGURES 173, 174. *Austrocneiphia tonnoiri* male. (173) Dorsal view. Lectotype. (Lesmurdie). Image by LHG-A. Scale bar = 0.5 mm. (174) Habitus. Arrow indicates wing spot (w s). (Kangaroo Gully). Scale bar = 1.0 mm.



FIGURES 175–179. *Austrocnephia tonnoiri* male. (175) Frontal view of head. (Kangaroo Gulley). Scale bar = 0.2 mm. (176) Wing spot. Scale bar = 0.1 mm. (177) Ventral view of genitalia. Paralectotype. Scale bar = 0.05 mm. (178) Gonocoxa (gc), gonostylus (gs), paramere (p) and spines (s). (Serpentine). Scale bar = 0.05 mm. (179) Genitalia, slide mounted, basal arms (ba), parameres (p), paramere connector (pc), ventral plate (vp). Paralectotype. Scale bar = 0.05 mm. **FIGURE 180.** *A. tonnoiri* pupa. (180) Female cephalic capsule. (Serpentine). Scale bar = 0.2 mm.



FIGURES 181–183. *Austrocnephia tonnoiri* pupa. (181) Male cephalic capsule. (Serpentine). Scale bar = 0.2 mm. (182) Gill. Some filament tips broken. (Serpentine). Scale bar = 0.2 mm. (183) Habitus. Female pupa. (Stony Brook). Scale bar = 1.0 mm.

Types. Drummond did not designate a holotype, but labeled material as co-types. Subsequent labeling, probably by the Mackerras', designated a holotype and an allotype. Bugledich (1999: 329) followed suit listing a male holotype, plus one male and four female paratypes. Under present Code, the former should be referred to as the 'Lectotype'; the others as 'Paralectotypes'.

Lectotype. Pinned male. Examined by LHG-A in 2007 and photographed (Fig. 173). Type locality Western Australia, Lesmurdie (S31.9900° E116.0500°). 18 Oct. 1930. Coll. F. H. Drummond. (Fig. 195). Exact labeling not recorded.

Paralectotypes. Two pinned specimens examined. Male, head missing. Label data:- [From pupa/ Lesmurdie/ 18. 10. 30/ Coll. F. H. D.] [Co-type *Simulium/ tonnoiri*] [*Simulium/tonnoiri* {M}/ Drum/ Paratype] [Red card] [Aust. Nat./ Ins. Coll.]. Now as microscope slide. Female, same labels, but with {F}.

Additional material. A single specimen is housed in the medical entomology collection, Westmead Hospital, Sydney. Label:- [Species number 01002B1H7] [Lab number (79-1640)] [*Cnephia tonnoiri tonnoiri*] [01/10/29,] [Tillyard] [Lesmurdie Plains, WA]. This predates Drummond's collection and is assumed here to be the original

discovery of the species, that which led Drummond to collect at Lesmurdie a year later. He made no comment. The specimen was not examined.

Alcohol material: All stages; collected variously by D. Bedo, H. & P. Zwick and JKM. [ANIC Database No./ 29 026532–026539; 29 026746; 29 026750; 29 026847]; [UASM# 370822–370826]. *Slide mounts:* All stages [UASM# 370807–370821]

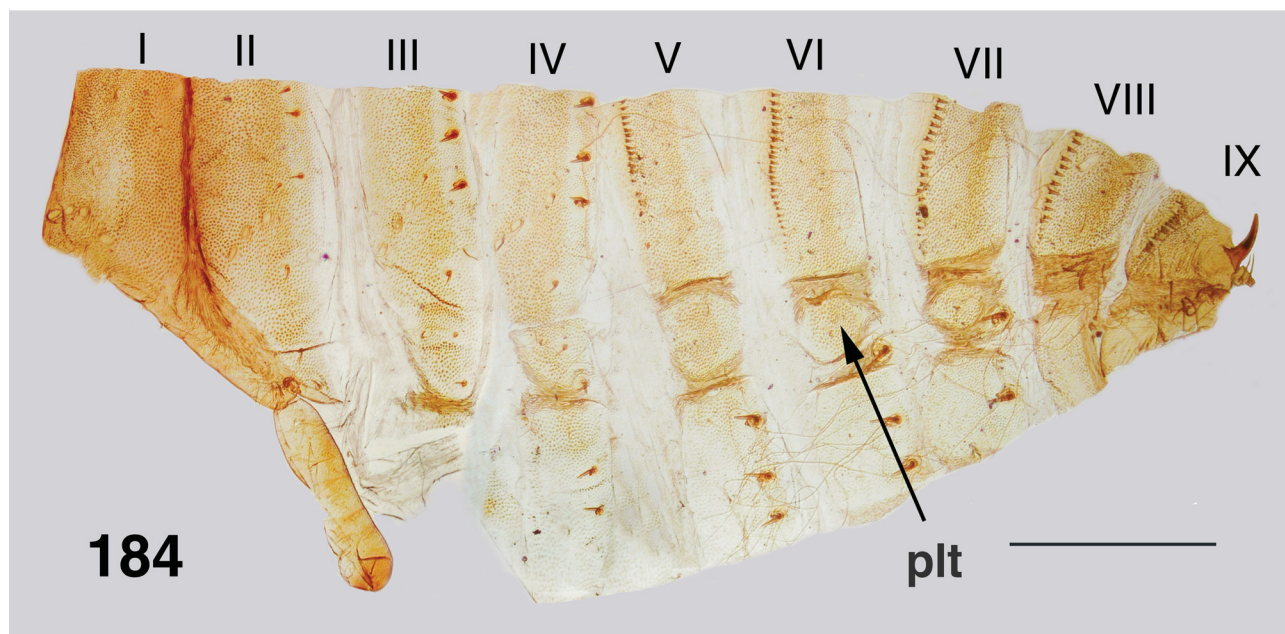


FIGURE 184. *Austrocnechia tonnoiri* pupa. (184) Abdominal armature. Arrow indicates pleurite (plt). (Serpentine). Scale bar = 0.5 mm.

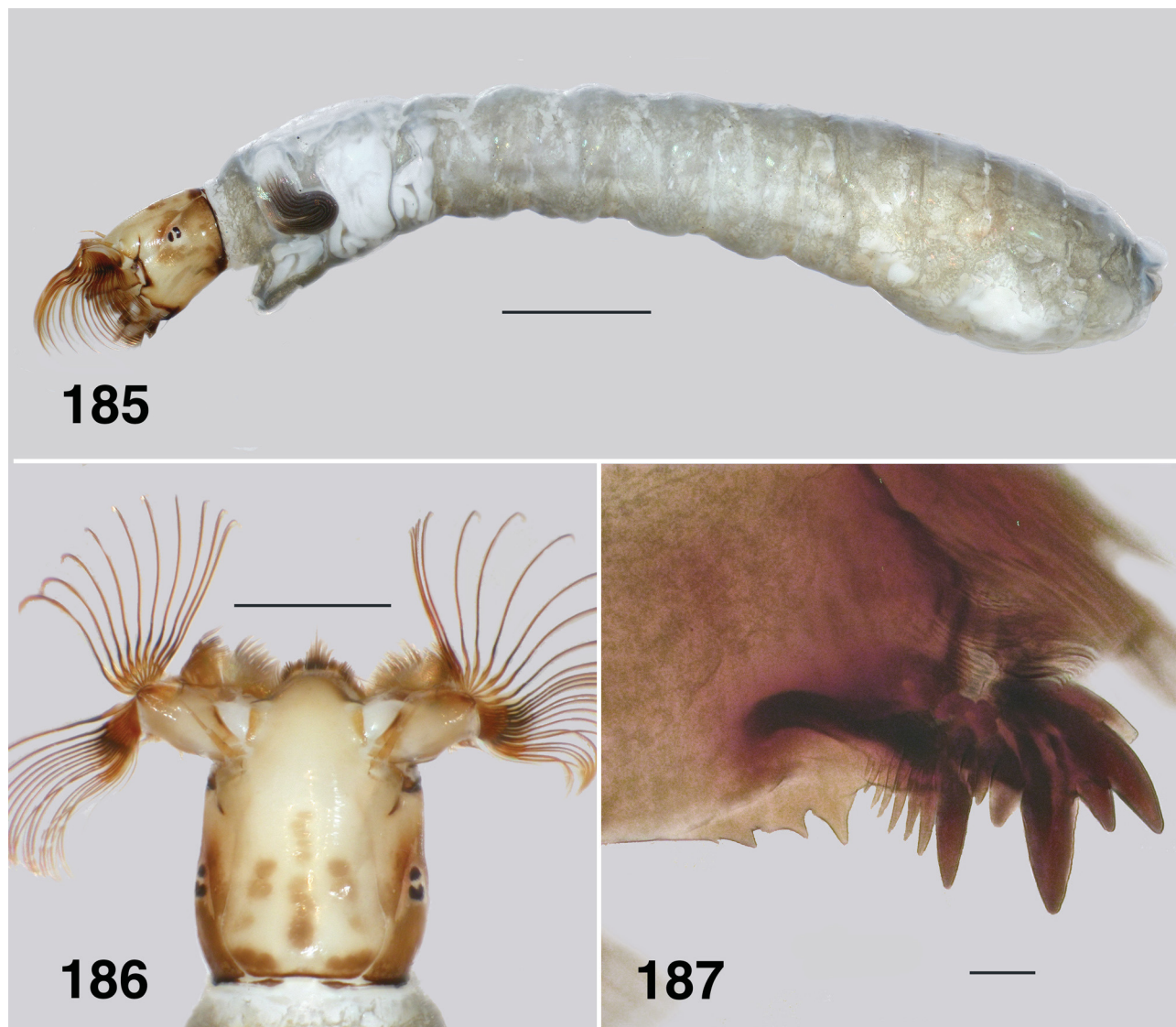
Bionomics. Drummond (1931: 8) and Mackerras & Mackerras (1949: 384) noted that *A. tonnoiri* breeds in a wide range of stream types. Drummond (*loc. cit.*) commented that pupae often form clumps with only the posterior tip of the cocoon attached—a behaviour reminiscent of pupae for the *aurantiaca* species-group. Behaviour of adults is unknown—we assume that the female is non-biting of humans, at least; an assumption supported partly by the markedly small teeth only on the medial side of the female mandible.

Prince (1980) in an ecological study of simuliids in Jane Brook, a small stream in the Darling Range, WA, found that larvae of *Austrocnechia tonnoiri* were present from March until December, with peak numbers in March. Fast flow and rocky substrate were attributes of the habitats. No adults were ever taken in the field. *Austrosimulium furiosum*, *A. bancrofti* and *Simulium ornatipes* occurred in the same stream reach. *Simulium ornatipes* was, however, largely separated in time, being more common in the summer and *A. furiosum* preferred the slower flows.

Distribution (Fig. 197). *Western Australia.* Near Perth, Bullsbrook, S31.6700° E116.0300°. 16 Aug. 1953. Four adults. Coll. D.L. McIntosh (ANIC). Jane Brook, S31.8808° E116.0862°. (Prince, 1980). Walyunga National Park. S31.7300° E116.0600°. 26 May 2007. Larvae. Coll. L. Gil-Azevedo (ROM). Perth, S31.9400° E115.8500°. July 1930. Two adults. Coll. Drummond. 15 Nov. 1924. 20 adults. Coll. Nicholson (ANIC). South of Perth, Serpentine Falls, S32.3690° E116.0065°. 26 Oct. 2002. Larvae, pupae. Coll. Zwick (ANIC). Lesmurdie, S31.9900° E116.0300°. 9 Dec. 1949. Larvae, pupae. Coll. D. Saunders (ANIC). Lesmurdie, S31.9900° E116.0300°. Oct. 1949. Pupae and larvae. Coll. Unknown (ANIC). Lesmurdie Fall, S31.9951° E116.0333°. Sept. 1929. Pupae. Coll. A. Tillyard (ANIC). Lesmurdie Plains, S32.0000° E116.0500°. 1 Oct. 1929. Coll. Tillyard (WMH). Jarrah Forest, Brookton Highway, Route 40, Kangaroo Gulley, S32.1181° E116.1527°. 7 Nov. 1996. Larvae, pupae, reared adults. Coll. J.K. Moulton (UASM). Kelmscott, Route 40, Brookton Highway, Stoney Brook, S32.1250° E116.0472°. 14 Nov. 1996. Pupae, reared adults. Coll. J.K. Moulton (UASM). Near Perth, Canning Dam, Kangaroo Gulley, S32.1480° E116.1210°. 11 Jul. 1971. Larvae. Coll. D. Bedo (ROM). Wungong Brook, S32.1921° E116.0081°. Aug. Larva. Coll. Nicholson (ANIC). South of Perth, Serpentine River, S32.3700° E 116.0000°. Mar. 1972. Pupae. Coll. Zwick (ANIC). Pinjarra, east of Waroona. Lane Poole Reserve, Icy Creek, S32.8090° E116.0950°. Oct 2005. Larvae. Coll. Zwick (ANIC). Harvey, S33.0760° E115.9052°. Mar. 1972. Larvae. Coll. Zwick (ANIC). Margaret River, S33.9400° E115.0700°. 10 Nov. 1958. Adult. Coll. E.F. Riek (ANIC). NW Pemberton, Donnelly River, S34.1070° E115.9900°.

Mar. 1972. Larvae, pupae. Coll. Zwick (ANIC). Stirling Ranges, Moingup Springs, S34.4100° E 118.1500°. 28 Oct. 2005. Larvae, pupae. Coll. Zwick (ANIC). Beedelup National Park, Carey Brook, S34.4100° E115.8000°. Mar. 1972. Pupae. Coll. Zwick (ANIC). Beedelup National Park, Beedelup Falls, S34.4186° E115.8688°. 1972. Larvae. Coll. Zwick (ANIC). Beedelup Falls, S34.4186° E115.8688°. 13 Nov. 1958. Five adults. Coll. E.F. Riek (ANIC).

Prince (1980; her Fig. 3) mapped some 70 localities for *A. tonnoiri*, from north of Perth to Stirling Range National Park, southern Western Australia, but detailed localities were not given.



FIGURES 185–187. *Austrocnephia tonnoiri* larva. (185) Habitus, last instar. (Kangaroo Gully). Scale bar = 1.0 mm. (186) Dorsal view of head, last instar. (Kangaroo Gully). Scale bar = 0.5 mm. (187) Mandible apex. (Harvey). Scale bar = 0.02 mm.

Remarks. Mackerras & Mackerras (1949: 380, 384) originally considered material from Canberra and Coree Ck., ACT, as *A. tonnoiri*, but subsequently (Mackerras & Mackerras, 1950: 170) restricted distribution to Western Australia and considered that the then *Cnephia tonnoiri* consisted of three subspecies, *tonnoiri*, *orientalis* and *fuscoflava*.

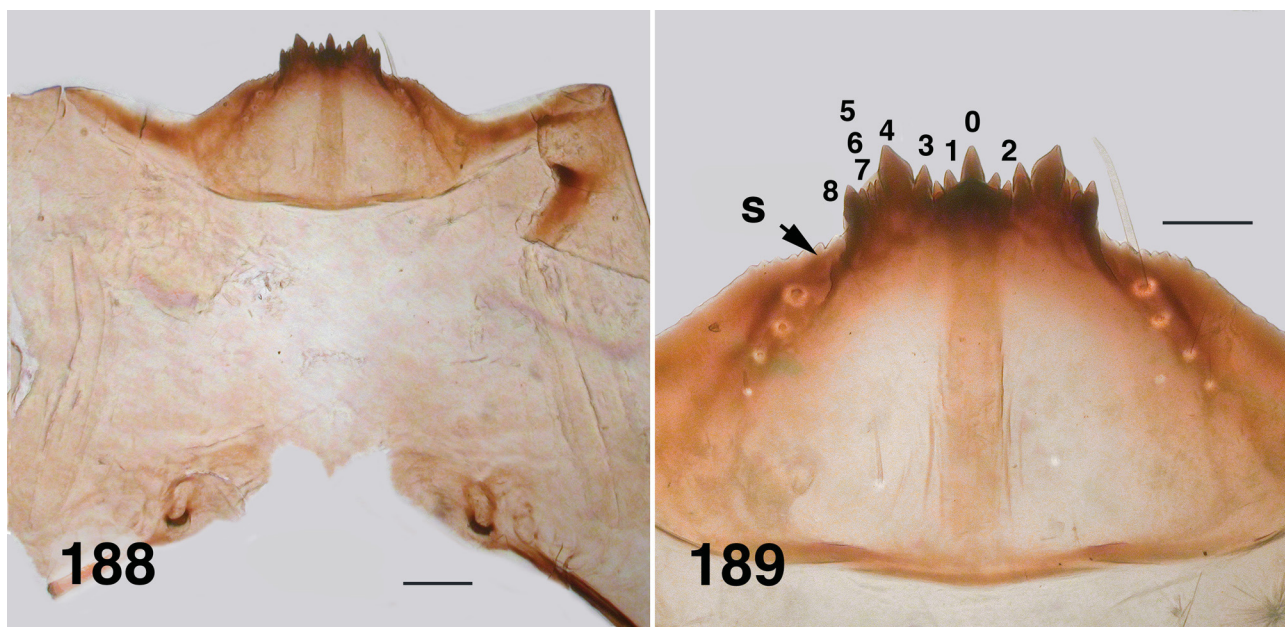
Rothfels (1979) in a cytological examination of Australian *Austrocnephia* (as *Cnephia* at the time), stated that *A. tonnoiri* occurred not only in Western Australia, but also Tasmania. That distribution has been cited since (e.g., Crosskey & Howard, 1997: 18). Of note was that *A. tonnoiri* consisted of two chromosomal siblings, but it is not clear if they were separate in Western Australia and Tasmania. This latter point is of biogeographical interest, since no material of *A. tonnoiri* is currently known from Tasmania, given the broadly-based collections (see Distribution(s) given) that have been made there. *Austrocnephia orientalis* is, however, widely distributed. Is it possible that *A. orientalis* of Tasmania is more closely related to the Western Australian *A. tonnoiri* than to *A. orientalis*

on the neighbouring mainland? Certainly, larvae of Tasmanian *A. orientalis* are distinct from populations on the mainland, as noted previously.

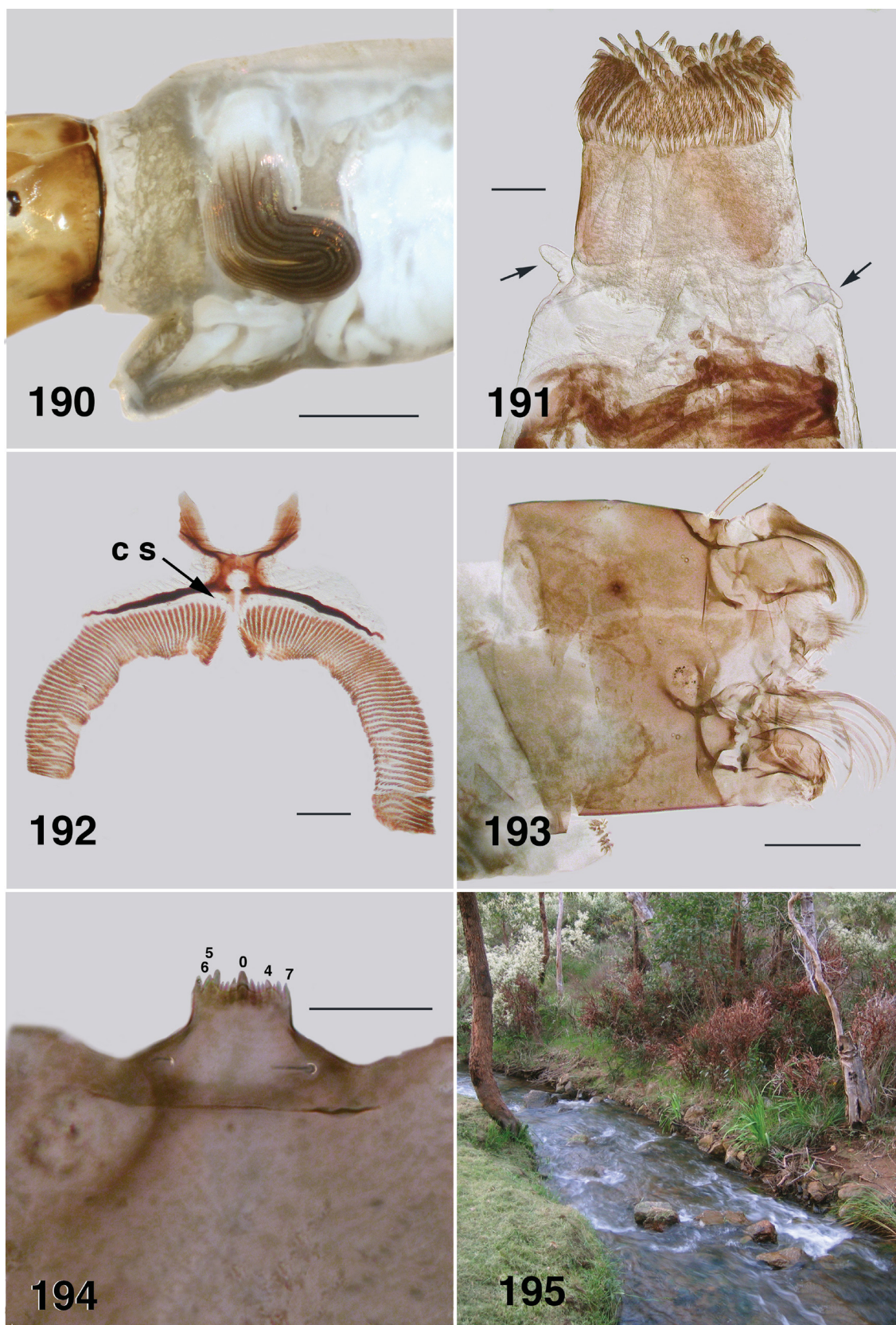
Further, in none of the Mackerras' work is *C. tonnoiri* recorded as occurring in Tasmania. Indeed, they comment that *Cnephia* material from the peninsula south of Adelaide, South Australia, was not as might be expected of *C. tonnoiri tonnoiri* from Western Australia, but was of the eastern *C. tonnoiri orientalis*. Prince (1980: 71) also does not report *A. tonnoiri* (as *C. tonnoiri tonnoiri*) occurring in Tasmania. Thence, we are of the opinion that the records of *A. tonnoiri* in Tasmania are, for the present, in error. Bugledich (1999: 329) too has *A. tonnoiri* present in eastern Australia—again in error?

Colbo (1974) described and illustrated the head of a first instar larva of *Cnephia tonnoiri orientalis*—now *Austrocnephia orientalis*. That, similar to first instar *A. tonnoiri*, dealt with already, possesses labral fans, clearly indicating that, as he noted, these species are not Prosimuliini. The hypostoma is similar in first instar larvae of both species (Figs. 161, 194), showing a developmentally plesiomorphic arrangement for those teeth. Similarly, Craig (1975: 466, 1997: 890) showed that highly apomorphic hypostomal teeth in Tahitian larval simuliids, have, in their first instar larvae, a very similar basic arrangement to that shown here—indicative perhaps that this is a plesiomorphic arrangement for Simuliini larval hypostomas? Be that as it may, Colbo (1974: 123) illustrated hypostomas of *Austrosimulium bancrofti* and *Aust. pestilens* first instar larvae, expressed both as in their respective mature larvae and not in the suggested plesiomorphic state as above.

Drummond (1931: 4) in discussing predators of Australian simuliids, commented that for *A. tonnoiri*, where the pupa are clumped and accumulate material, chironomid larvae were often present in and around the cocoons. He suggested that perhaps the chironomid larvae were preying on the simuliids, but in a footnote, comments that Tonnoir suggested the chironomids were merely commensals. We too have noted presence of chironomid larvae in the pupal mats and tend to agree with Tonnoir. Drummond (*loc. cit.*) further commented that cocoons of *A. tonnoiri* are very rough with a wide array of foreign material incorporated (Fig. 183). Also, that when the cocoons are clumped, often in groups of 10 or more, only the posterior of the cocoon is attached to the substrate (we too have noted this arrangement for *aurantiaca* and *strenua*). Cocoons are usually found on stones, rarely on grass, in both fast and slow water (Fig. 195). Also noted was the dichromatic condition of the female eye (Fig. 166) and the marked pigmentation at the r-m veins junction (Fig. 176). That latter character, consists of campaniform sensillae located at the base of Rs, plus a concentration of pigmented hairs on R₁ and slight pigmentation of the wing membrane; producing the appearance of three closely adjacent pigment spots.



FIGURES 188, 189. *Austrocnephia tonnoiri* larva. (188) Ventral head cuticle. (Jane Creek). Scale bar = 0.1 mm. (189) Hypostoma. Arrow indicates serrations (s). (Jane Creek). Scale bar = 0.05 mm.



FIGURES 190–194. *Austrocnephia tonnoiri* larva. (190) Pupal gill histoblast. (Kangaroo Gully). Scale bar = 0.5 mm. (191) Prothoracic proleg showing small lappets (arrows). (Harvey). Scale bar = 0.05 mm. (192) Anal sclerite and circlet of hooks. Arrow indicates campaniform sensilla (c s). (Harvey). Scale bar = 0.1 mm. (193) Head of 1st instar larva. (Serpentine). Scale bar 0. = 05 mm. (194) Hypostoma, 1st instar larva. (Serpentine). Scale bar 0. = 02 mm. **FIGURE 195.** *Austrocnephia tonnoiri* type locality. (195) Lesmurdie Stream, WA. Sept. 2005. Image courtesy of Creative Commons.

Biogeography

Austrocnephia species have a clear-cut east-west distribution with four species occurring along much of the length of eastern Australia and one species (*A. tonnoiri*) from north of Perth to southeastern Western Australia (Prince, 1980). Similarly *Nothogreniera fergusoni* and *N. occidentalis* (Mackerras & Mackerras) (see Craig *et al.*, 2018b) for which all stages are now known, are eastern and western respectively. Then too, the Western Australia *Ectemnoides* species with their sister taxon *Ect. umbratorum* (Tonnoir) in south-eastern Australia (Moulton *et al.*, 2018) and similarly, eastern *Paraustrosimulium colboi* (Davies & Györkös) with *Protaustrosimulium pilfreyi* (Davies & Györkös) (see Craig *et al.*, 2017 & Currie *et al.*, 2018 respectively) matched with western sister taxa. Such distributions are well known for other biota of Australia and have been examined extensively (e.g., Keast, 1981; Unmack, 2001, 2013; Byrne *et al.*, 2008; Yeates *et al.*, 2009; Byrne *et al.*, 2011; Rix & Harvey, 2012; Rix *et al.*, 2015). The gap in distribution for *Austrocnephia* occurs between the Adelaide Peninsula, South Australia and the vicinity of Beedelup National Park, Western Australia—some 2,000 km.

In relation to the “Interim Biogeographic Regionalization for Australia, Version 7” (IBRA) regions (e.g., Taylor *et al.*, 2018)—in Queensland, *A. strenua* occurs northerly in the Wet Tropics (WT) region, with well-to-the-south populations in the South Eastern Queensland (SEQ) region, then Sydney Basin (SYB) plus the South Eastern Highland (SEH) regions of Victoria and New South Wales. For *A. aurantiaca*, apart from a suspect outlier population in Northern Queensland, the remaining populations occur in a variety of southeastern regions and southwest out to the Victoria Midlands (VM) region. For *A. orientalis*, there are again suspect outlier populations in Northern Queensland and inland in the Brigalow Belt South (BBS) region, with populations variously along the east and southeast of the continent and in the Kanmantoo (KAN) region, near Adelaide, South Australia. *Austrocnephia fuscoflava* is known only from the South Eastern Queensland (SEQ) region. *Austrocnephia tonnoiri* in Western Australia is restricted to the Swan Coastal Plain (SWA), Jarrah Forest (JAF), Warren (WAR) and westerly part of the Esperance Plains (ESP) regions. Trayler *et al.* (1996), in discussing conservation of aquatic fauna of the Warren bioregion, noted that rivers of the south-western corner of Australia arise on an ancient flat semi-arid plateau and flow sluggishly towards the coast. There is then steeper topography and increased rainfall, coastal lowlands and lagoons. They listed, however, only *Austrosimulium furiosum* and *Austrocnephia tonnoiri* (as *Cnephia tonnoiri tonnoiri*) in the region—a considerably poorer list of simuliids than now known. Be that as it may, the above distributions of the various species need more information regarding conditions favourable to each taxa—details of value to biogeographic considerations.

During the Cretaceous Aptian-Albian (125–99 Mya) and before Australia fully separated from Antarctica, a central continental Eromanga Sea flooded in from northern Australia, broke out of the continent to the east near Brisbane, to the northwest and also south central at the present Nullarbor Plain, that then abutted the developing rift valley between Australia and Antarctica (Thompson & Stillwell, 2010). Given that we know, from superb fossils, that simuliids were present in Australia at that time (Jell & Duncan, 1986), it is possible that this southern extension of the Eromanga Sea was the original barrier between the east and west simuliid populations of Australia?

The present Nullarbor Plains and the Great Victoria Desert to the north have not, however, always been inimical to simuliids, immatures of which require running fresh water. While the Plains are amongst the largest uncovered area of limestone known (Webb & James, 2006), it was exposed during the Early Oligocene (ca. 30 Mya) for some 10 my, then re-inundated by the sea in the Late Oligocene (23 Mya). Current withdrawal of the sea took place in the mid-Miocene (ca. 14 Mya) and soon after that the whole region was uplifted through tectonic activity. Of possible significance is that Unmack (2001, 2013) illustrated what he referred to as ‘bathymetric rivers’ draining off the continental shelf in the Australian Bight, when sea levels were depressed; perhaps providing dispersal routes for simuliids? Toussant *et al.* (2016) in a study of secondarily terrestrial Australian diving beetles (*Paroster* Sharp) considered that the optimal period (MMCO or mid-Miocene climate optimum) for aquatic organisms was between 17–14.5 Mya (see also Woodhead *et al.*, 2016). This is in general agreement with Unmack (2001) who was of the opinion that present day distribution and endemism of freshwater fish in Australia was determined by climatic changes since the Miocene (23–5 Mya), with more recent events of minimal influence. By the late Miocene (7 to 6 Mya) the Nullarbor Plains region was drying and at ca. 5 Mya vegetation was similar to that of today. The current markedly arid climate has been so for the last 1 my. The area is, however, famous for its karst formation and caves—indicating that there were periods of wetter climate with river channels (Martin *et al.*, 2003; Webb & James, 2006). Indeed, in late- to mid-Eocene (40–30 Mya) the climate of the overall region apparently supported monsoon woodland (Byrne *et al.*, 2008). A recent, wide-ranging study including fossil pollen records from radiometrically

dated stalagmites (Sniderman *et al.*, 2016), showed that prior to the very late Miocene (*ca.* 5.5 Mya) the Nullarbor Plains were arid, with similar rainfall as present. However, by *ca.* 5.0 Mya, there was a rapid shift to less arid conditions with vegetation more adapted to mesic (wetter) conditions. This period of greater precipitation continued for *ca.* 1.5 my until the late Early Pliocene (*ca.* 3.5 Mya). For Simuliidae, an assumption could be made that this was the latest period when exchange between western and eastern fauna might have taken place, arguably with running water present at the time. The morphological character differences between the two fauna indicate, however, that such an exchange did not take place recently.

In similar vein, Austin *et al.* (2004) in a major overview of Australian insect diversity, suggest that present day distributions of the insect fauna largely reflect climate changes of gradual drying since the Late Pleistocene imposed on earlier patterns—the common thread in Australian historical biogeography. Byrne *et al.* (2008) and Byrne *et al.* (2011) examined the development of Australian arid and mesic zones. In the latter work they tested various hypotheses using modern data for Australian biota. The definition of the mesic zone used (their Fig. 1) fits closely the distribution of *Austrocnephia*—not surprising given that simuliid immatures require running water. The hypothesis best supported was one where the ancestral biota of Australia was mesic. In a reconstruction of the paleoclimates of Australia they indicate that prior to the early Oligocene (33 Mya) there was relatively good water availability over much of the continent, but then drying of the climate commenced, with fluctuations, as in part noted previously here. So, timing of the east-west splits of various segregates of Australian Gondwanan simuliid fauna is moot—we are, however, again, of the opinion that the split was not recent.

Preference for cool to cold fast water by larvae of many *Austrocnephia* species is probably integral to paleoclimates of Australia and presence of mountain ranges in the current eastern mesic region as defined by Byrne *et al.* (2011), which largely follow the Great Dividing Range. These mountains started formation during the Hunter-Bowen Orogeny; a significant arc accretion event in the Permian and Triassic periods (299–199 Mya) affecting approximately 2,500 km of the Australian eastern continental margin. While the Great Dividing Range north and west of Sydney is presently a prominent landform, this is the end result of crustal uplift since the Jurassic with several episodes of deformation, accretion, subduction and magmatic activity, with the mountains overall now severely eroded from their original heights. Clearly, with adequate altitude and rainfall, fast flowing water has been available for a long period of time for immatures of precursor *Austrocnephia* to adapt to fast colder water; in particular those of *A. aurantiaca* and *A. strenua*.

Tasmania has ancient underpinnings. Western Tasmania and King Island to the northwest have geologic formations dated at Proterozoic–Cambrian age (1,000–510 Mya). Further, geological similarities and connections of Tasmania to mainland Australia in Victoria and New South Wales are part of the ‘Tasmanides’ (Rosenbaum, 2018), an area along eastern Australia that was influenced by active plate boundaries from the Cambrian to the Triassic (541–201 Mya). These geological configurations extend south-east beyond the South Tasmania Rise.

The suggestion earlier that perhaps *A. aurantiaca* of Tasmania and Flinders Island are separate species from that on the mainland is in good agreement with the geological history of this part of Australia. As mentioned earlier, again, superb fossil larvae of yet undescribed Simuliidae are known from the Koonwarra Fossil bed to the SE of Melbourne (Jell & Duncan, 1984); well dated at 116 Mya (Aptian Age of middle Early Cretaceous) and, given the marked gestalt of the fossil larvae to those of extant Simuliidae, it is clear that this is a minimum age and that the Family was in this part of Gondwana well before the Aptian. Indeed, definitive fossils of adult simuliids are known elsewhere (Kalugina, 1991) from the Upper Jurassic/ Lower Cretaceous (151–137 Mya); plus Currie & Adler (2008: 472) have suggested the origin of Simuliidae to be of Pangean Age (*i.e.*, Middle Jurassic–Early Carboniferous; 335–175 Mya).

Break up of Gondwana and in particular the separation of Australia from Antarctica have been heavily studied and, as Exon *et al.* (2002) stated, this is “*One of the great stories of geoscience.....*”. Of caution though is that placement of terrains and timing of events are controversial (White *et al.*, 2013). Briefly, in the Early Jurassic (200 Mya) proto-Australia was well connected to Antarctica with ‘Tasmania’ plus the South Tasmanian Rise situated between the Australian plate and that of East Antarctica. Northward movement of Australia away from Antarctica commenced in the Cretaceous beginning from the west; forming what would become the Australo-Antarctic Gulf (AAG) along the southern edge of the-to-be Australian continent. At the time the fossil simuliids were extant (116 Mya), breakup was well underway. The Ocean Drilling Program (OCP) Leg 189 (Exon *et al.*, 2004) shows that by 95 Mya (Late Cretaceous), there was sedimentation in the AAG between ‘Tasmania’ and the ‘Australia’ mainland—the origin of the Bass Strait. Such sedimentation filled various deepening basins in the region. Perhaps this

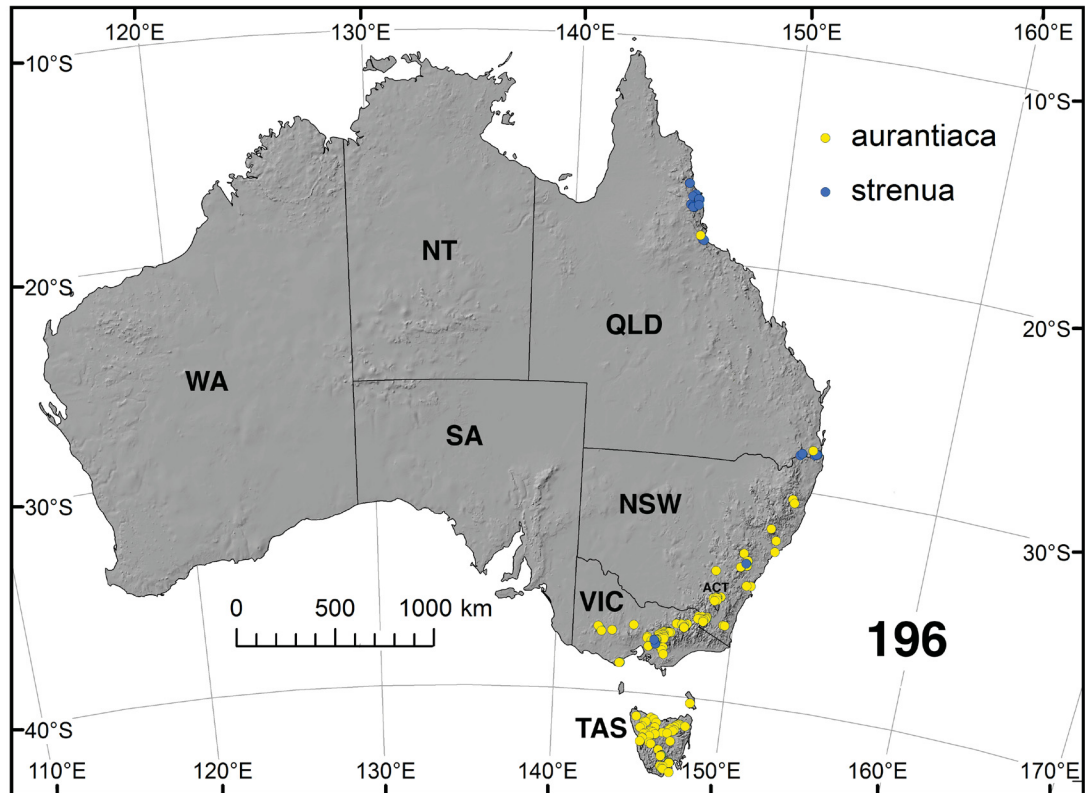


FIGURE 196. Distribution of *Austrocnephia aurantiaca* species-group (*A. aurantiaca*, *A. strenua*).

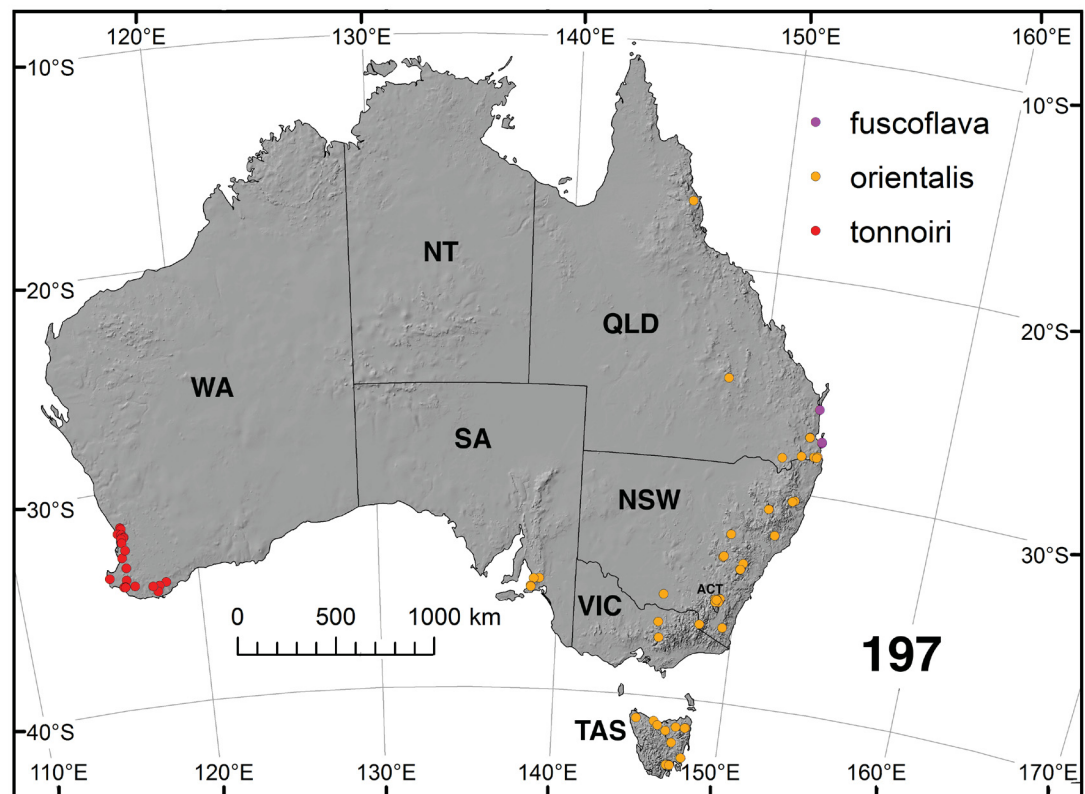


FIGURE 197. Distribution of *Austrocnephia tonnoiri* species-group (*A. fuscoflava*, *A. orientalis*, *A. tonnoiri*).

was the vicariant event that produced divergence of proto-*Austrocnephia aurantiaca* into the current forms? The main rifting of the Antarctic, Australia and Campbell Plateau tectonic plates continued to the southeast. Tasmania was still joined to East Antarctica at 65 Mya and did not become separated completely until *ca.* 33.5 Mya, with the Tasmania Gateway fully opened at 26 Mya (Exon *et al.*, 2002; Exon *et al.*, 2004), allowing formation of the Antarctic Circumpolar Current (ACC) resulting in marked consequences for local and planetary climate with the now isolated Antarctica.

The Bass Strait is relatively shallow—a drop in sea level of a mere 50 m would extend Flinders Island almost half way to mainland Victoria. The depression of sea level of 135 m, as in the Last Glacial Maximum, exposed a large area of relatively flat land (Unmack *et al.*, 2013: 31) with the center region occupied by ‘Bass Lake’ and westward drainage of waterways from the higher land ranged along the extreme east of the plain. With low topographical relief, flowing water was likely slow.

The five species of *Austrosimulium* reported as occurring on Tasmania (Mackerras & Mackerras, 1952: 113), are *A. cornutum*, *A. bancrofti*, *A. furiosum*, *A. victoriae* and *A. torrentium torrentium* Tonnoir. Many of these are widespread on mainland Australia and immatures are quite tolerant of a wide array of running water habitats. Reaching Tasmania via the waterways of an exposed Bass Strait when exposed during various sea level depressions is a not unreasonable suggestion. Dumbleton (1973 : 559), however, commented that given morphological differences, the Tasmanian exemplars of *Austrosimulium* may well be eventually shown as separate species from those on the Australian mainland—indicating considerable time of separation?

For the other genus of Simuliidae in Australia, namely *Simulium*, it is generally assumed (*e.g.*, Dumbleton, 1973: 561, Williams, 1980: 237, Craig *et al.*, 2006: 20), as noted earlier, that its precursors entered Australia from South East Asia, perhaps sometime after 40 Mya in the mid-Eocene. With one exception—*S. ornatipes*—all other Australian *Simulium* species are endemic. Colbo (1974: 267) showed that while many of these species are distributed north in Queensland, across the Northern Territories with one species in northern Western Australia, others are well distributed along the east of the continent. While *Simulium melatum* Wharton, occurs near Melbourne and in the Gippsland region—presence of *Simulium* is unknown for Tasmania. Does this indicate an arrival in SE Australia when the Bass Strait was inundated or otherwise inimical?

Tyler’s Line (Shiel *et al.*, 1989) in Tasmania is considered a biogeographic phenomenon based on major geological difference between the east and west of the island. Rees & Cwynar (2010) demonstrated that the underlying geology has an effect on distribution of Chironomidae, correlated with pH of the water. Distribution of *A. orientalis* in Tasmania may show such an effect since the species occurs mainly in the eastern part of the island (Fig. 197); on the other hand, *A. aurantiaca* is widespread, albeit mainly to the north and west (Fig. 196). We have, however, no information on pH of the habitats of these larvae, so for the present suggest that the differing requirements of temperature and velocity of the water, needed by the immature stages, determines distribution. Craig *et al.* (2012: 190) showed, for New Zealand, that pH of running water habitats while higher in the North Island than the South, there was nothing to suggest that this determined species distribution of *Austrosimulium* between, or within, these two main islands. Larvae of Australian mainland *Austrocnephia aurantiaca* prefer fast colder water, which in Tasmania is found more to the west, however, also elsewhere. Larvae of *A. orientalis* are found in warmer slower flows, which occur more to the east. Both habitat conditions are mediated by the underlying geology—more mountainous to the west, less so in the east.

Williams (1980, 1981) and Zwick (1981a, b) in general overviews of Australian aquatic insects, while reiterating the older nature of Plecoptera and Blephariceridae (Diptera) fauna, did not deal with detailed historical biogeography.

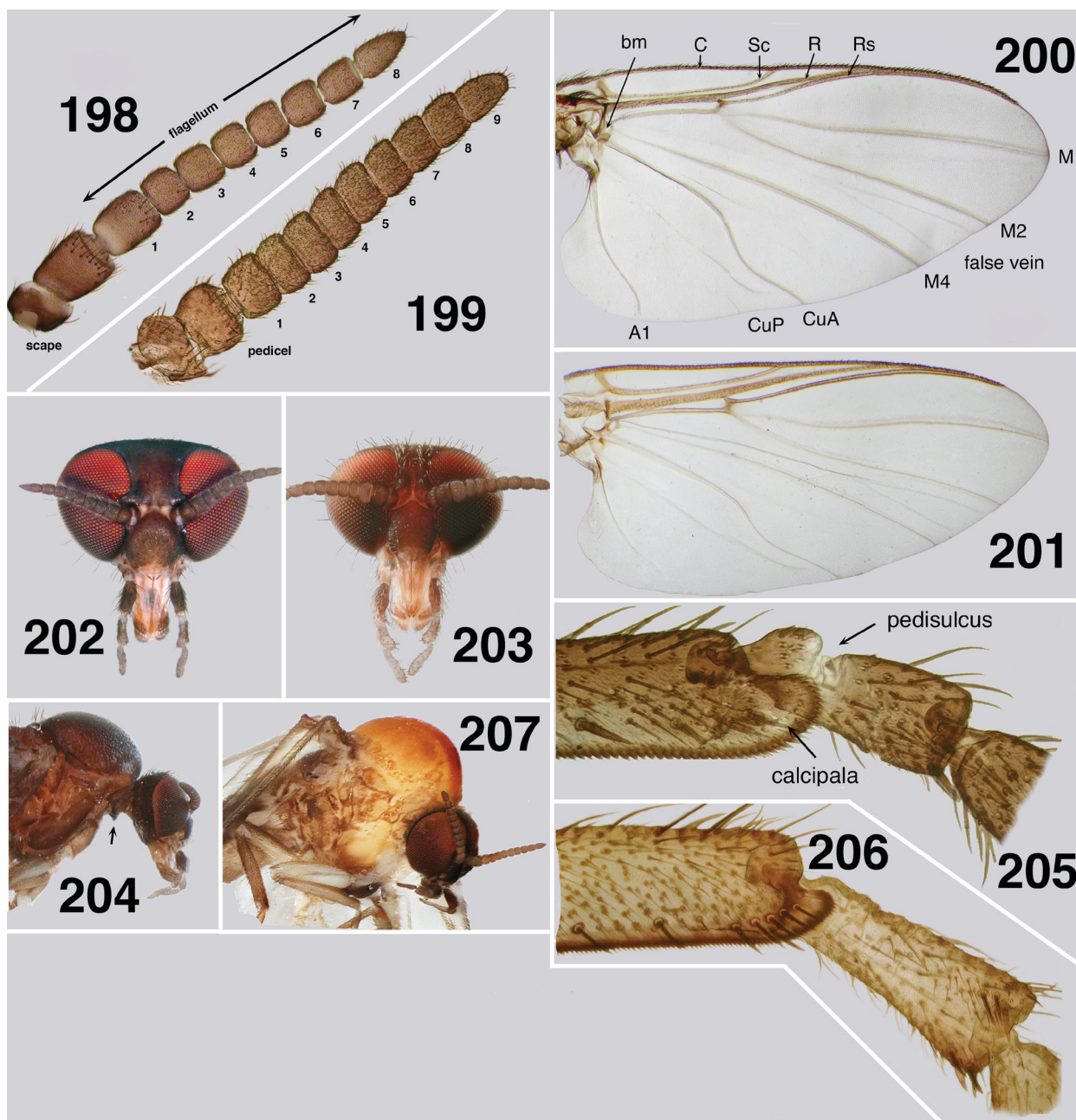
Key to genera of Australian Simuliidae

(Figs. 8–10, 65, 198–240)

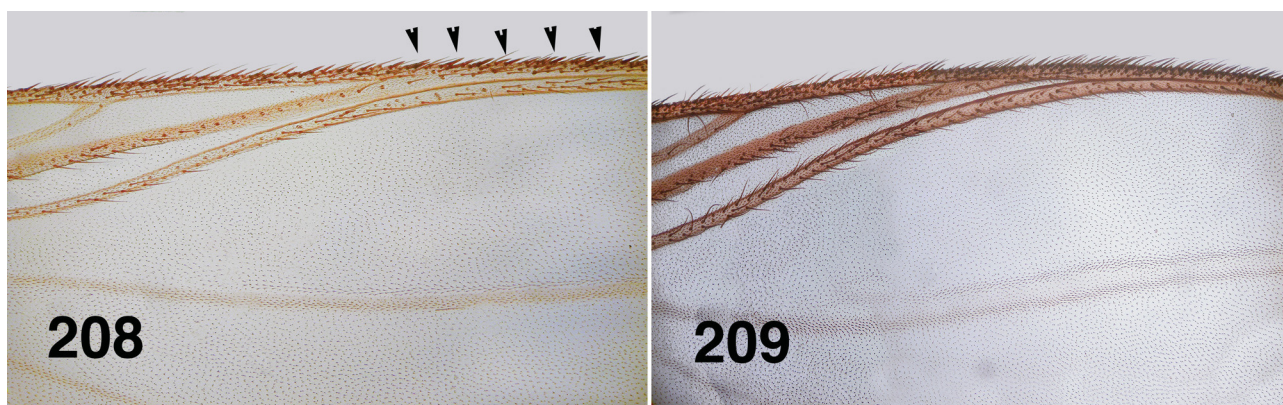
This key is based on the life stages of the Australian black flies known to us. The following species are unknown in two or more life stages: *Ectemnoides uvulatus* (female, male), *Protaustrosimulium terebrans* (male, pupa, larva), *Protaustrosimulium opscurum* (male, pupa, larva),

Adults

1. Antennal flagellomeres 8 [8 or 9 in *Austrosimulium bancrofti* (Taylor)] (Fig. 198); apices of R₁ and Rs closely appressed before joining C (Fig. 200) 2
- Antennal flagellomeres 9 (Fig. 199); apices of R₁ and Rs closely appressed, or not (Fig. 201), before joining C 3
2. Frons of female wide (Fig. 202), thorax domed, cervical sclerites not markedly expressed *Austrosimulium*
- Frons of female narrower (Fig. 203), thorax not markedly domed, cervical sclerites markedly expressed (Fig. 204) *Paraustrosimulium*

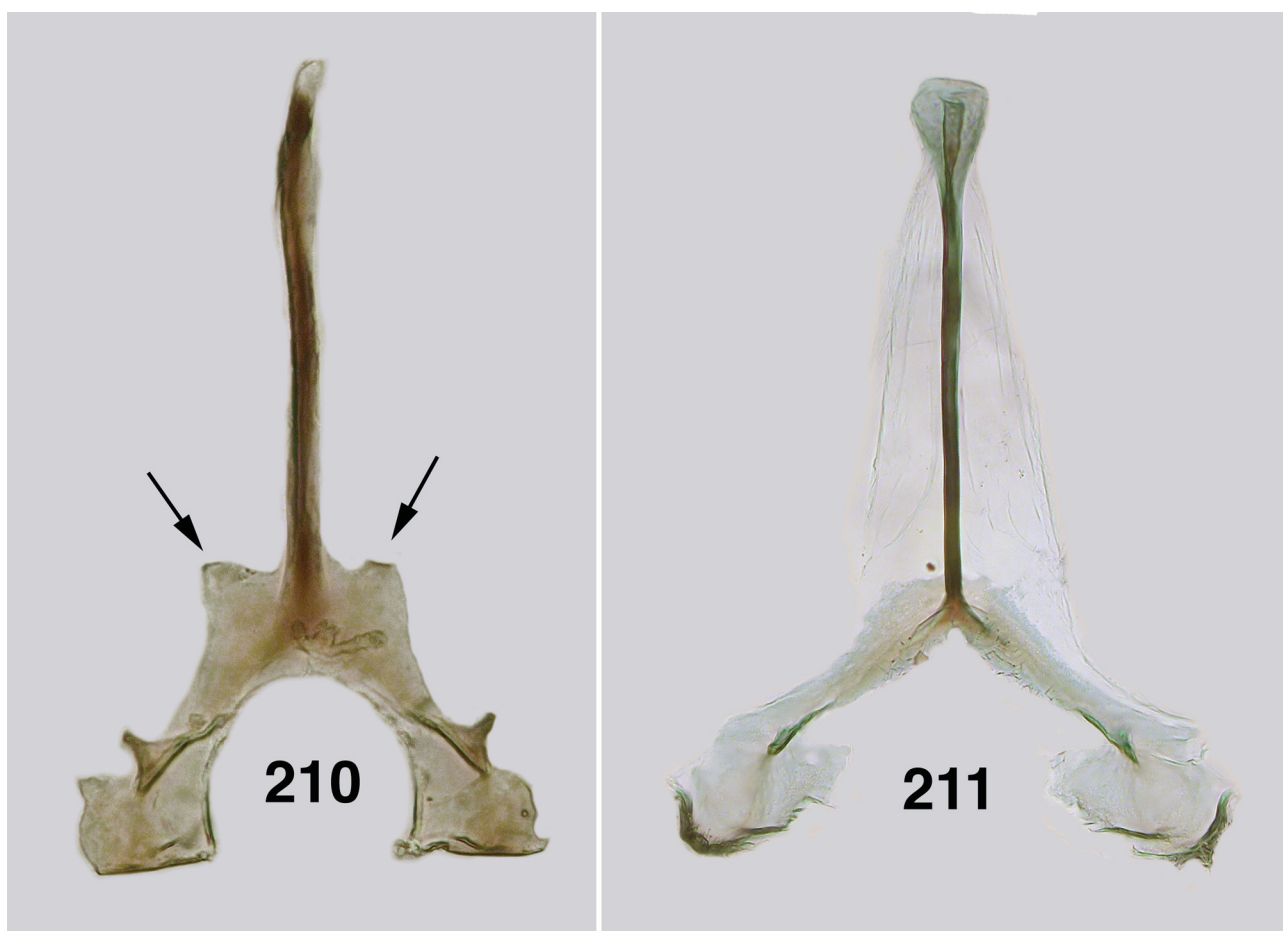


FIGURES 198–207. (198) *Austrosimulium* sp., female antennae, showing number of flagellomeres. (199) *Bunyipellum gladiator* (Moulton & Adler), female antennae, showing number of flagellomeres. (200) *Austrosimulium montanum* Mackerras & Mackerras, wing of female, showing appressed veins R & Rs. (201) *Bunyipellum gladiator*, wing of female, veins R & Rs not appressed. (202) *Austrosimulium* sp., frontal view of female head showing width of frons. (203) *Paraustrosimulium colboi* (Davies & Györkös), frontal view of female head showing width of frons. (204) *Paraustrosimulium colboi*, lateral view of female adult, showing dark scutum. Arrow indicates distinct cervical sclerites. (205) *Simulium dycei* Colbo, female hind leg showing spines, calcipala and pedisulcus. (206) *Bunyipellum gladiator*, female hind leg showing spines and calcipala. (207) *Austrocnephia aurantiaca*, scutum of female.



FIGURES 208, 209. (208) *Ectemnoides umbratorum* Moulton, Currie and Craig, female, anterior wing veins. Arrowheads indicate spine-like setae on costa. (209) *Nothogreniera fergusoni* (Tonnoir), female, anterior wing veins. Note absence of spine-like setae.

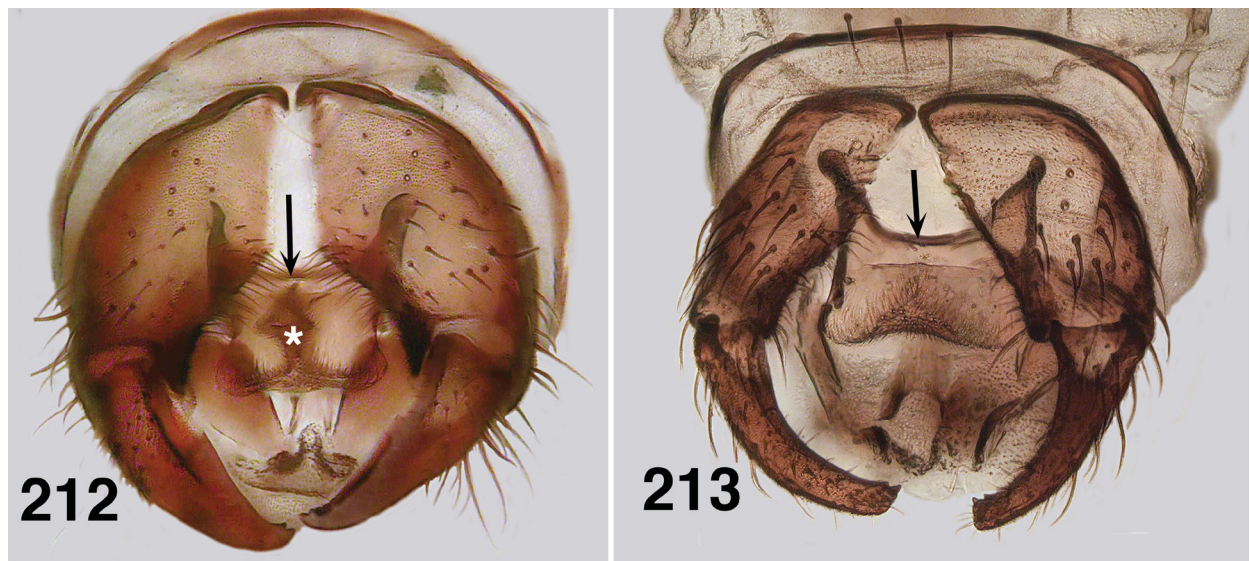
- | | | |
|----|--|---------------------------|
| 3. | Apices of R_1 and R_s closely appressed before joining C (Fig. 200) | <i>Protaustrosimulium</i> |
| - | Apices of R_1 and R_s not closely appressed before joining C (Fig. 201) | 4 |
| 4. | Pedisulcus present as a single deep groove (Fig. 205); bm cell absent | <i>Simulium s.l.</i> |
| - | Pedisulcus absent or represented at most by a series of shallow grooves or wrinkles (Fig. 206); variously-sized bm cell present (Figs. 200, 201) | 5 |



FIGURES 210, 211. (210) *Ectemnoides umbratorum*, genital fork. Arrows indicate apodemes. (211) *Nothogreniera fergusoni*, genital fork.

- | | | |
|----|--|---|
| 5. | Scutum bright yellow-orange (Fig. 207) | 6 |
| - | Scutum gray to black (Fig. 204) | 7 |

6. Calcipala large, lamellate, its base almost as wide as hind basitarsus apex (Fig. 10); pedisulcus represented by series of shallow grooves (Fig. 65); Rs branched or thickened apically (Figs. 8, 9) *Austrocnephia* n. gen.
- Calcipala small, its base one-third or less width of hind basitarsus apex; pedisulcus absent, represented at most by slightly wrinkled cuticle (Fig. 206); Rs unbranched, not thickened apically (Fig. 201) *Bunyipellum*
7. Costa with dark, spine-like setae interspersed among longer, paler hair-like setae (the former more prevalent near the apex of costa) (Fig. 208); calcipala large, its base half or more width of hind basitarsus apex (e.g., Fig. 205) *Ectemnoides* (in part)
- Costa with only pale setae, some of which may be short and stiff but neither dark nor fully spiniform (Fig. 209); calcipala small, its base a third or less width of hind basitarsus apex (e.g., Fig. 206) 8
8. Female 9
- Male 10
9. Arm of genital fork with large lateral triangular anteriorly-directed apodemes (Fig. 210) *Ectemnoides*
- Arm of genital fork without anteriorly directed apodemes (Fig. 211); if apodemes present, then small and laterally directed *Nothogreniera*
10. Ventral plate with midventral keel and a markedly produced hairsute lip (Fig. 212) *Nothogreniera*
- Ventral plate with neither a midventral keel nor a markedly produced hairsute lip (Fig. 213) *Ectemnoides*



FIGURES 212, 213. (212) *Nothogreniera fergusonii*, ventral view of genitalia. Arrow indicates ventral plate, * indicates midventral keel. (213) *Ectemnoides umbratorum*, ventral view of genitalia. Arrow indicates ventral plate, note absence of marked keel.

Pupae

1. Cocoon slipper- or shoe shaped (Fig. 214); in doubtful cases terminal spines minute (Fig. 217) 2
- Cocoon a loosely woven sac of indefinite shape (Fig. 215); in doubtful cases terminal spines well developed (Fig. 216) 6
2. Gill with threadlike filaments arising from single hornlike stalk (Fig. 218); abdominal tergites V–VIII without anterior row of spine combs (Fig. 217) *Austrosimulium*
- Gill either a single annulated club lacking filaments (Fig. 219), or with multiple primary trunks that may or may not bear secondary filaments; abdominal tergites V–VIII with spine combs on one or more segments (Fig. 216) 3
3. Gill a single, inflated, annulated, cone-like process without secondary filaments (Fig. 219) *Paraustrosimulium*
- Gill varied in structure, but consisting of multiple, non-annulated primary trunks; secondary filaments present or absent. 4
4. Gill with 10 filaments (Fig. 220); Western Australia *Protaustrosimulium* (in part, *Prot. amphorum*)
- Gill with 8 or fewer filaments; variously distributed 5
5. Gill with 6 whitish, semi-translucent, tubular filaments that extend horizontally from base (Fig. 221) *Protaustrosimulium* (in part, *Prot. pilfreyi*)
- Gill with 4–8 filaments of various form (Fig. 222); if gill with 6 inflated filaments, then these extended vertically from base (e.g., Fig. 223) *Simulium* s.l.
6. Gill with 18 (rarely 20) or fewer filaments 7
- Gill with 21 or more filaments 9
7. Gill with filaments arising from 2 or 3 markedly elongated common stalks (Fig. 224); gill as long as (or longer than) pupal body; in doubtful cases pleuron of abdominal segment IX with apically curved setae *Ectemnoides* (in part)
- Gill with filaments arising from a various number of shorter common stalks (Fig. 225); gill typically shorter than pupal body; in doubtful cases pleuron of abdominal segment IX with grapnel-shaped setae 8

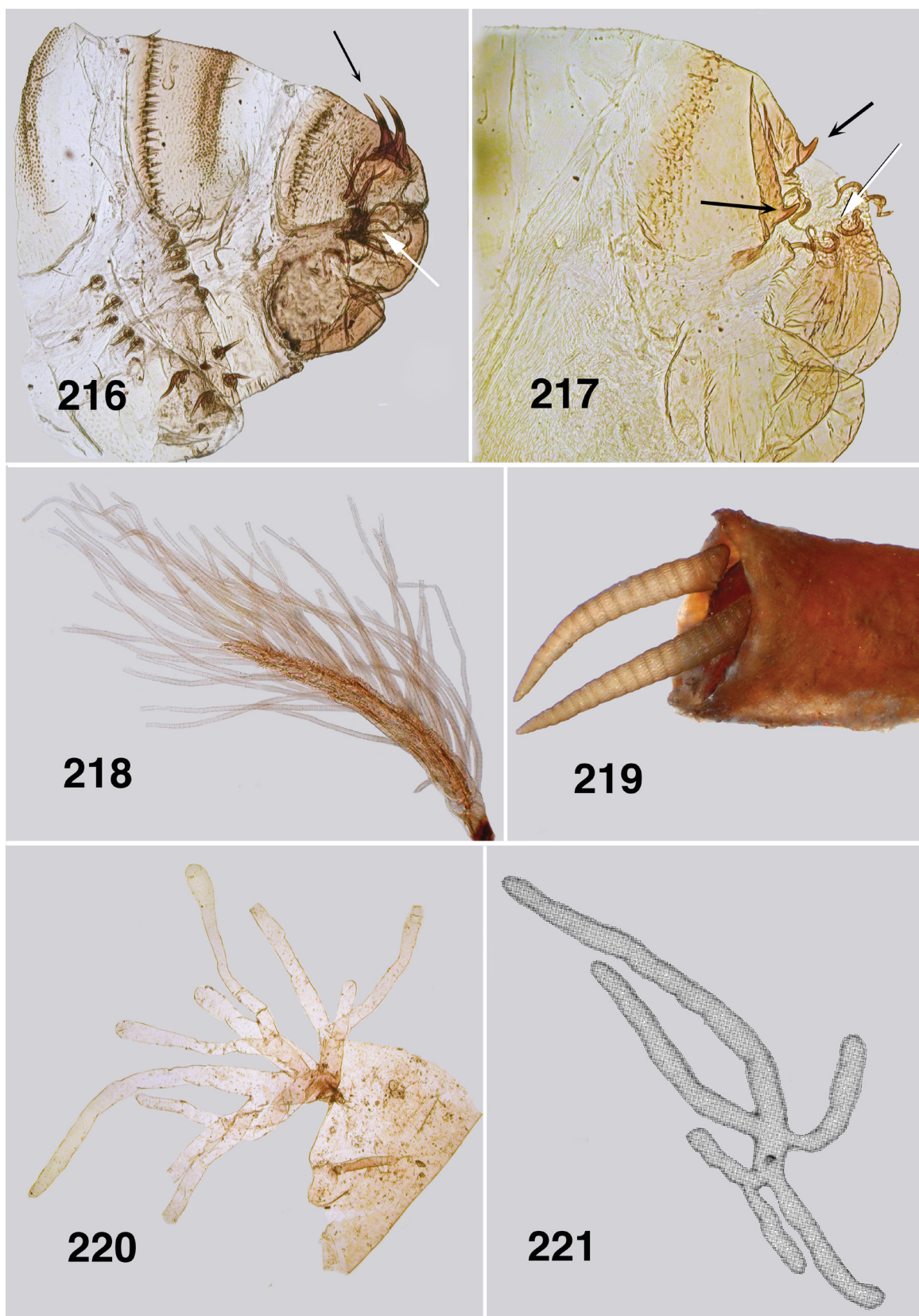
8. Abdominal segment V with seta-bearing pleurite (if present) essentially joined to tergite V (Fig. 226); pleuron of abdominal segment IX with apically curved setae. *Ectemnoides* (in part)
- Abdominal segment V with seta-bearing pleurite clearly separated from tergite V (Fig. 227); pleuron of abdominal segment IX with grapnel-shaped setae. *Nothogreniera*
9. Thorax not markedly domed (e.g., Fig. 215); dorsocentral setae elongated, spine-like, darkly pigmented; gill with ca. 50 gill filaments (Western Australia). *Bunyipellum*
- Thorax markedly domed (Fig. 28), dorsocentral setae trichoid and more lightly pigmented; gill with 21-50 gill filaments (widely distributed) *Austrocnephia* n. gen.



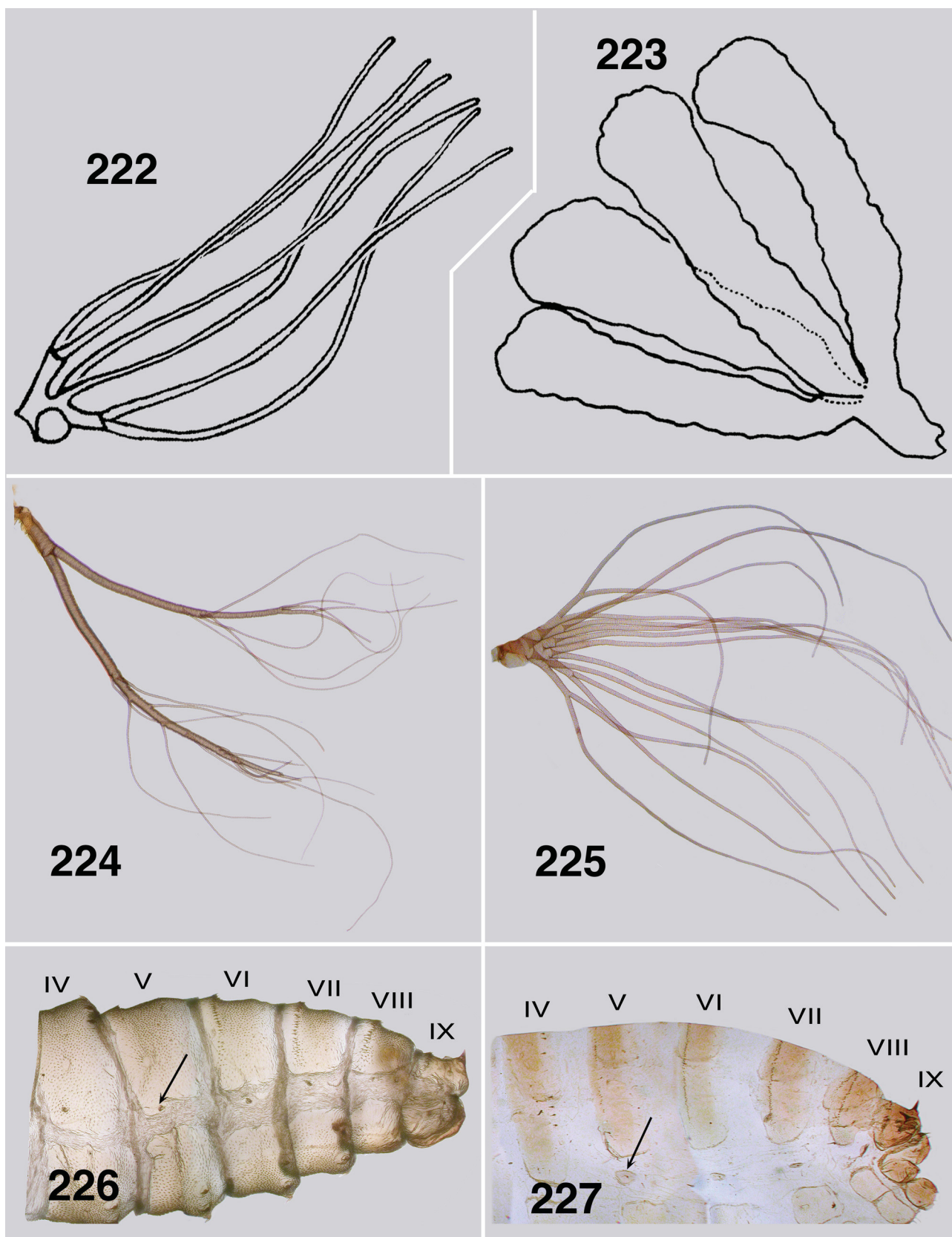
FIGURES 214, 215. (214) *Austrosimulium bancrofti* (Taylor), male pupa showing shoe-shaped cocoon. (215) *Ectemnoides princeae* Moulton, Craig & Currie, showing indefinite shape cocoon.

Larvae

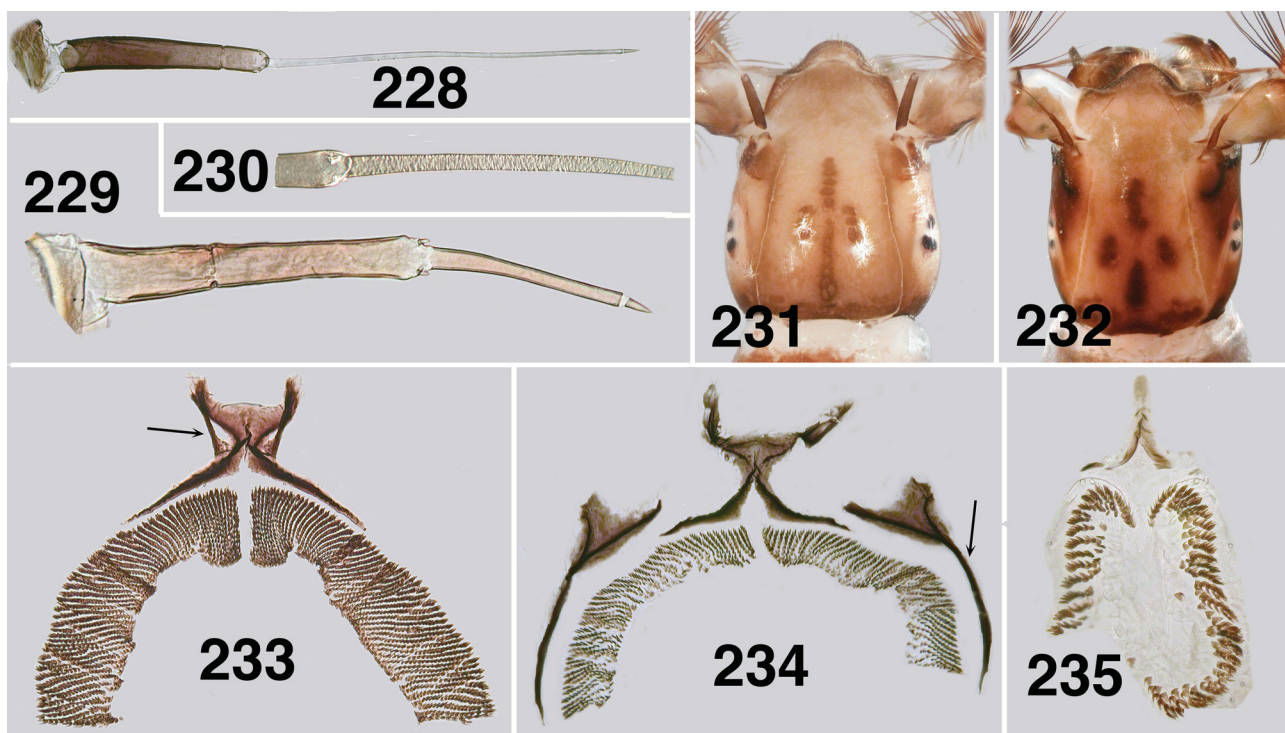
1. Antenna with apical article equal in length to, or longer than, basal and medial articles combined; medial article typically less than 1/3 length of basal article (Fig. 228) (in doubtful cases apical article without fine bands as in Fig. 230); anteromedial and posteromedial head spots nearly continuous (Fig. 231). 2
- Antenna with apical article shorter than basal and medial articles combined; if subequal in length, then medial article conspicuously longer than 1/3 length of basal article (Fig. 229) (in doubtful cases apical article with fine bands as in Fig. 230); anteromedial and posteromedial head spots widely separated (Fig. 232) 5
2. Anal sclerite with lateral inter-arm strut between anterior and posterior arms (Fig. 233); postgenal cleft more strongly developed, its apex triangular, rounded, or quadrate in shape 3
- Anal sclerite without lateral inter-arm strut between anterior and posterior arms (Fig. 234); postgenal cleft at most a narrow slit that extends anteriorly ca. 1/8th distance to hypostomal groove. *Protaustrosimulium*
3. Semicircular sclerite absent (Fig. 233). 4
- Semicircular sclerite present (e.g., Fig. 234) *Austrosimulium* (*Austrosimulium*)
4. Antenna with apical article shorter than basal and medial articles combined (Fig. 229); gill histoblast with threadlike filaments arising from single stalk (Fig. 236) *Austrosimulium* (*Novaustrosimulium*)
- Antenna with apical article longer than basal and medial articles combined (Fig. 228); gill histoblast a concertinaed annulated cone-like process without secondary filaments (Fig. 237). *Paraustrosimulium*
5. Hypostomal teeth arranged on 3 prominent lobes, with teeth 0 and 1 on median lobe and teeth 3–7 on lateral lobes (Fig. 238); apical antennal article with fine bands (Fig. 230) *Nothogreniera*
- Hypostomal teeth not arranged on three 3 prominent lobes (although untoothed lateral lobes sometimes present as in Fig. 240); apical antennal article without bands (e.g., Fig. 229). 6
6. Labral fan stem wider than long, with 75–88 strongly developed rays; anterior margin of hypostoma concave, with apex of tooth 0 extended anteriorly no farther than apex of tooth 1 (Fig. 239); (Western Australia). *Bunyipellum*
- Labral fan stem longer than wide, with a varied number of normally developed rays; anterior margin of hypostoma not markedly concave, in doubtful cases apex of tooth 0 extended anteriorly farther than tooth 1 (e.g., Fig. 240); (widely distributed). 7
7. Anal sclerite X-shaped, with both anterolateral and posterolateral arms present (Fig. 234) 8
- Anal sclerite either absent or in the form of an inverted Y, with only the posterolateral arms present (Fig. 235). . . *Ectemnoides*
8. Body rather stocky with evenly distributed dark grey to dark brown pigmentation; head light- to dark brown, with cervical sclerites typically joined to postocciput via a narrow strap; antenna shorter than labral fan base, with medial and distal articles more darkly pigmented than basal article; prothoracic proleg with a darkly pigmented lateral plate that extends nearly the entire length of distal article, in some species with a pair of lateral lappets *Austrocnephia* n. gen.
- Body of more typical form with head and body pigmentation varied; cervical sclerites free, not connected with postocciput; antenna varied in length and color, but not as described above; prothoracic proleg with lateral plate inconspicuous, lappets absent *Simulium* s.l.



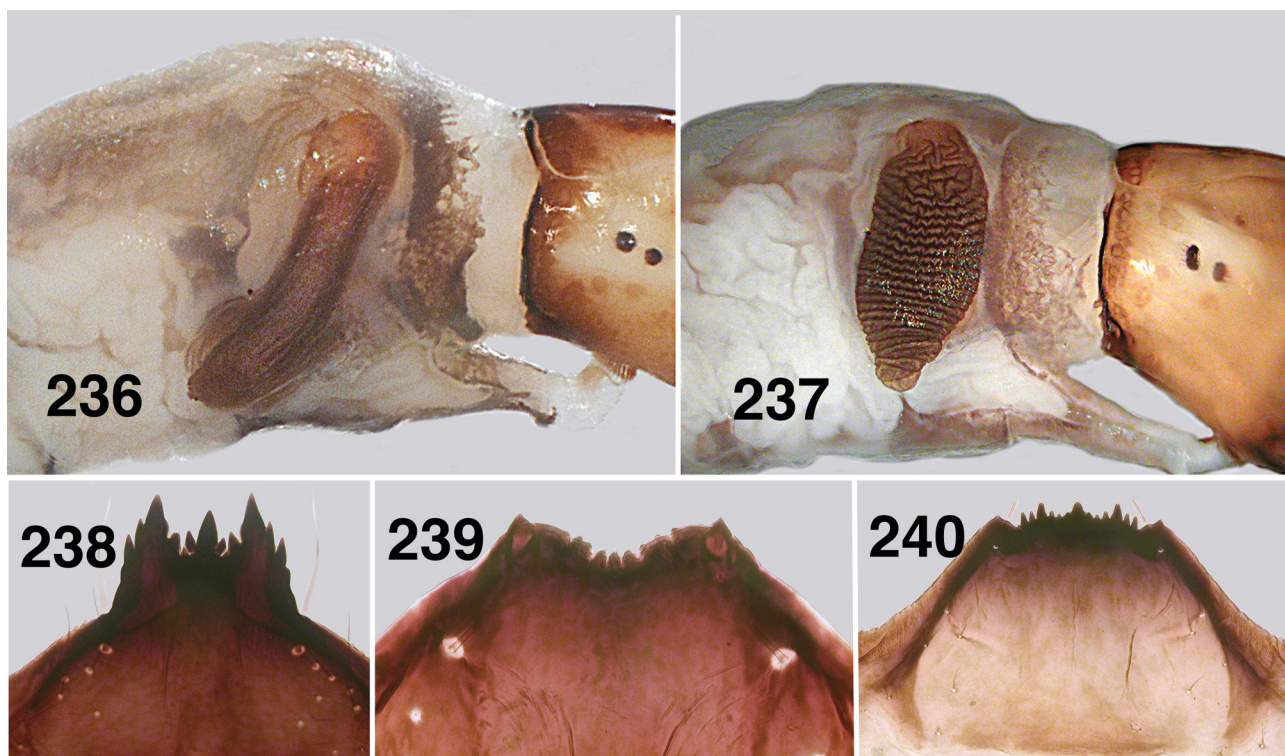
FIGURES 216–221. (216) *Bunyipellum gladiator*, terminal pupal abdomen. Black arrow indicates large terminal spines, white apically curved setae. (217) *Paraustrosimulium colboi*, terminal pupal abdomen. Black arrows indicate small terminal spines, white grapple hook setae. (218) *Austrosimulium (Novaustrosimulium) pestilens* Mackerras & Mackerras, pupal gill. (219) *Paraustrosimulium colboi*, pupal gill. (220) *Protaustrosimulium obcidens* Currie, Craig & Moulton, pupal gill. (221) *Protaustrosimulium pilfreyi* (Davies & Györkös), pupal gill—modified from Davies & Györkös, 1988.



FIGURES 222–227. (222) *Simulium faheyi* Colbo, pupal gill—modified from Colbo, 1976. (223) *Simulium standfasti* Colbo, pupal gill—modified from Colbo, 1976. (224) *Ectemnoides acanthocranius* Moulton, Currie & Craig, pupal gill. (225) *Nothogreniera fergusonii* (Tonnoir), pupal gill. (226) *Ectemnoides acanthocranius*, pupal abdomen. Arrow indicates fused pleurite (227) *Nothogreniera fergusonii*, pupal abdomen. Arrow indicates separate pleurite.



FIGURES 228–235. (228) *Protostrosimulium amphorum* Craig, Currie, Moulton; antenna of larva. (229) *Austrosimulium* (*Novaustrosimulium*) *bancrofti* (Taylor); antenna of larva. (230) *Nothogreniera fergusonii*, distal antennomere showing banding. (231) *Protostrosimulium amphorum*, larval head showing spot pattern. (232) *Nothogreniera fergusonii*, larval head showing spot pattern. (233) *Austrosimulium* (*Novaustrosimulium*) *bancrofti*, anal sclerite. Arrow indicates inter-arm strut. (234) *Protostrosimulium amphorum*, anal sclerite. Arrow indicates semicircular sclerite. (235) *Ectemnoides umbratorum* (Tonnoir), showing reduced anal sclerite.



FIGURES 236–240. (236) *Austrosimulium* (*Novaustrosimulium*) *bancrofti*, larva, showing pupal gill histoblast. (237) *Paraustrosimulium colboi*, larva, showing pupal gill histoblast. (238) *Nothogreniera fergusonii*, hypostoma. (239) *Bunyipellum gladiator*, hypostoma. (240) *Ectemnoides absitus* Moulton, Craig & Currie, hypostoma.

Epilogue

Long referred to as the ‘*Cnephia*’ of Australian authors, this group of primitive-grade simuliids represent a heterogeneous assemblage not assignable to either of the other two genera known from Australia: viz., *Austrosimulium* Tonnoir and *Simulium* s.l. Latreille. Crosskey & Howard (1997) transferred the ‘*Cnephia*’ species to the African genus *Paracnephia* Rubtsov based on a perceived similarity in labral fan structure between one of the African species (*thornei*) and one of the Australian species (*strenua*). However, other specialists expressed reservations about the relationship of these Australian species to *Paracnephia* s.s. and to each other (e.g. Moulton *et al.*, 2004; Gil-Azevedo & Maia-Herzog, 2007; Currie & Adler, 2008).

With this, the 6th and final contribution in a series focusing on the Gondwanan simuliids of Australia, the genus *Paracnephia* is no longer recognized on that continent, and the Australian species previously assigned to that taxon are now distributed among six genera as follows: *Paraustrosimulium* Wygodzinsky & Coscarón 1962; *Bunyipellum* Craig, Currie & Moulton 2018; *Ectemnoides* Moulton, Currie & Craig 2018; *Nothogreniera* Craig, Currie & Moulton 2018; *Protaustrosimulium* Currie, Craig & Moulton 2018; and *Austrocnephia* n. gen. Including *Austrosimulium*, *Simulium* s.l. and the new species described in the various revisions in this series, the simuliid fauna of Australia now stands at eight genera and 45 nominal species. The number of species is likely underrepresented given the dearth of taxonomic research over the last 60+ years. Only a handful of Australian simuliids have been studied cytologically to date, including just three of 20 nominal species dealt with in this series of revisions (cf. Rothfels, 1979 and Adler & Crosskey, 2015 for reviews). Among those, *Austrocnephia tonnoiri* is already known to be a species complex—a situation likely to be found in other species once they have been screened cytologically. Along similar lines, only three species of interest—*Nothogreniera fergusonii*, *Austrocnephia aurantiaca* and *A. orientalis*—have been DNA barcoded to date (Hernandez-Treana *et al.*, 2017). An integrated taxonomic approach using multiple sources of data offers the best hope for developing a sounder estimate of Australian simuliid diversity.

Much work remains to be done on higher-level relationships among Australian black flies. While it was beyond the scope of these studies to conduct a phylogenetic analysis of the Gondwanan simuliids as a whole, we consider monophyly of the genera described (or re-described) to be generally well supported—our caveats about the monophyly of *Protaustrosimulium* notwithstanding (Currie *et al.*, 2018). However, we are less certain about how these lineages are related to each other and to those from other zoogeographical regions. Evidence points to a shared ancestry between *Protaustrosimulium*, *Austrosimulium*, *Paraustrosimulium* and *Cnesiamima*—the latter of which is endemic to South America (Currie *et al.*, 2018). Beyond that, structural disparity among members of the other Gondwanan genera presents a challenge for morphology-based phylogeny reconstruction alone. Initial efforts using molecular data to resolve deep relationships within the Simuliidae produced mixed results (Moulton, 2000, 2003); however, recent advances in the genomic era offers hope that further insights can yet be gleaned. As with alpha-taxonomy, an integrated phylogenetic approach using multiple sources of data offers the best hope for untangling relationships among the Gondwanan genera of Australia.

This series of revisions has addressed the longstanding recognition that the Australian ‘*Cnephia*’ or ‘*Paracnephia*’ of authors was actually a highly diverse, polyphyletic, assemblage of Gondwanan origin. With the key herein provided to identify larvae, pupae and adults of Australian simuliids to genus level, we trust these revisions spark renewed interest on this fascinating, yet still understudied, group of organisms.

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References

- Adler, P.H. (2019) *World Blackflies (Diptera: Simuliidae): a comprehensive revision of the taxonomic and geographical inventory [2019]*. 139 pp. Available from: <http://www.clemson.edu/cafls/biomia/pdfs/blackflyinventory.pdf> (accessed 24 April 2019)
- Adler, P.H. & Crosskey, R.W. (2008) *World Blackfly (Diptera: Simuliidae): a fully revised edition of the taxonomic and geographic inventory*. 105 pp.
- Adler, P.H. & Crosskey, R.W. (2015) Cytotaxonomy of the Simuliidae (Diptera): a systematic and bibliographic conspectus. *Zootaxa*, 3975 (1), 1–139.
<https://doi.org/10.11646/zootaxa.3975.1.1>
- Adler, P.H., Currie, D.C. & Wood, D.M. (2004) *The Black Flies of (Simuliidae) of North America*. Royal Ontario Museum and Comstock University Press, Ithaca, 941 pp.
- Austin, A.D., Yeates, D.K., Cassis, G., Fletcher, M.J., La Salle, J., Lawrence, J.F., McQuillan, P.B., Mound, L.A., Bickel, D.J., Guilan, P.J., Hale, D.F. & Taylor, G.S. (2004) Insects 'Down Under'—Diversity, endemism and evolution of the Australian insect fauna: examples from select orders. *Australian Journal of Entomology*, 43, 216–234.
<https://doi.org/10.1111/j.1326-6756.2004.00448.x>
- Australian Government (2012) *Interim Biogeographic Regionalization for Australia. Version 7*. Available from: <https://environment.gov.au/land/nrs/science/ibra/australias-bioregions-maps> (accessed 24 April 2019)
- Bugledich, E.-M.A. (1999) Simuliidae. In: Wells, A. & Houston, W.W.K. (Eds.), *Diptera: Nematocera, Zoological Catalogue of Australia. Vol. 30.1*. CSIRO Publishing, Melbourne, pp. 325–337.
- Byrne, M., Yeates, D.K., Joseph, L., Kearney, M., Bowler, J., Williams, M.A.J., Cooper, S., Donnellan, S.C., Keogh, J.S., Leys, R., Melville, J., Murphy, D.J., Porch, N. & Wyrwoll, K.-H. (2008) Birth of a biome: insights into the assembly and maintenance of the Australian arid zone biota. *Molecular Ecology*, 17, 4398–4417.
<https://doi.org/10.1111/j.1365-294X.2008.03899.x>
- Byrne, M., Steane, D.A., Joseph, L., Yeates, D.K., Jordan, G.J., Crayn, D., Aplin, K., Cantrill, D.J., Cook, L.G., Crisp, M.D., Keogh, J.S., Melville, J., Moritz, C., Porch, N., Sniderman, J.M.K., Sunnucks, P. & Weston, P.H. (2011) Decline of a biome: evolution, contraction, fragmentation, extinction and invasion of the Australian mesic zone biota. *Journal of Biogeography*, 38, 1635–1656.
<https://doi.org/10.1111/j.1365-2699.2011.02535.x>
- Ciborowski, J.J.H. (1991) Head tube: a simple device for estimating velocity in running water. *Hydrobiologia*, 222, 109–114.
<https://doi.org/10.1007/BF00006098>
- Colbo, M.H. (1974) *Studies on the biology of the Simuliidae in north Eastern Australia: with reference to their potential as vectors of pathogens*. Ph. D. thesis, University of Queensland, Brisbane, 379 pp. Available from: <https://espace.library.uq.edu.au/view/UQ:366100> (accessed 24 April 2019)
- Colbo, M.H. (1976) Four new species of *Simulium* Latreille (Diptera: Simuliidae) from Australia. *Journal of the Australian Entomological Society*, 15, 253–269.
<https://doi.org/10.1111/j.1440-6055.1976.tb01703.x>
- Craig, D.A. (1974) The labrum and cephalic fans of larval Simuliidae (Diptera: Nematocera). *Canadian Journal of Zoology*, 52, 133–159.
<https://doi.org/10.1139/z74-017>

- Craig, D.A. (1975) Larvae of Tahitian Simuliidae (Diptera: Nematocera). *Journal of Medical Entomology*, 12, 463–476.
<https://doi.org/10.1093/jmedent/12.4.463>
- Craig, D.A. (1987a) A taxonomic account of the Black Flies (Diptera: Simuliidae) of the Society Islands—Tahiti, Moorea, Raiatea. *Quaestiones Entomologicae*, 23, 372–429. Available from: <https://www.biodiversitylibrary.org/page/51346944#page/399/mode/1up> (accessed 24 April 2019)
- Craig, D.A. (1987b) Some of what you should know about water. In: Titles and Abstracts, 35th Annual Meeting, North American Benthological Society, Orono, Maine, pp. 178–182. Available from: <http://w3.marietta.edu/~mcsaffd/aquatic/sextant/kiss.pdf> (accessed 24 April 2019)
- Craig, D.A. (1997) A taxonomic revision of the Pacific black fly subgenus *Inseliellum* (Diptera: Simuliidae). *Canadian Journal of Zoology*, 75, 855–904.
<https://doi.org/10.1139/z97-108>
- Craig, D.A. (2003) Geomorphology, development of running water habitats, and evolution of black flies on Polynesian islands. *Bioscience*, 53, 1079–1093.
- Craig, D.A., Craig, R.E.G. & Crosby, T.K. (2012) Simuliidae. *Fauna of New Zealand*, 68, 1–336. Available from: <https://bio-taxa.org/fnz/article/view/1840/3116> (accessed 24 April 2019)
- Craig, D.A., Englund, R.A. & Takaoka, H. (2006) Simuliidae (Diptera) of the Solomon Islands: new records and species, ecology, and biogeography. *Zootaxa*, 1328, 1–26.
- Craig, D.A., Moulton, J.K. & Currie, D.C. (2017) Taxonomic revision of *Paraustrosimulium* Wygodzinsky & Coscarón: re-assignment of *Austrosimulium colboi* and description of *P. obcidens* n. sp. from Western Australia. *Zootaxa*, 4337 (4), 451–492.
<https://doi.org/10.11646/zootaxa.4337.4.1>
- Craig, D.A., Currie, D.C. & Moulton, J.K. (2018a) Reassignment of Western Australia *Paracnephia gladiator* Moulton & Adler to a new genus, *Bunyipellum* (Diptera: Simuliidae). *Zootaxa*, 4375 (3), 341–357.
<https://doi.org/10.11646/zootaxa.4375.3.3>
- Craig, D.A., Currie, D.C. & Moulton, J.K. (2018b) *Nothogreniera* new genus, for two species of Australian “*Paracnephia*” (Diptera: Simuliidae). *Zootaxa*, 4444 (4), 351–380.
<https://doi.org/10.11646/zootaxa.4444.4.1>
- Crosby, T.K. (1974) Life history stages and taxonomy of *Austrosimulium* (*Austrosimulium*) *tillyardianum* (Diptera: Simuliidae). *New Zealand Journal of Zoology*, 1, 5–28.
<https://doi.org/10.1080/03014223.1974.9517810>
- Crosskey, R.W. (1969) A re-classification of the Simuliidae (Diptera) of Africa and its islands. *Bulletin of the British Museum (Natural History)*, 14, 1–195. Available from: <https://www.biodiversitylibrary.org/page/40874832#page/7/mode/1up> (accessed 24 April 2019)
- Crosskey, R.W. (1987) Part VIII. Black fly species of the world. 32 An annotated checklist of the world black flies (Diptera: Simuliidae). In: Kim, K.C. & Merritt, R.W. (Eds.), *Black Flies. Ecology, Population Management, and Annotated World List*. The Pennsylvania State University, University Park, pp. 425–520.
- Crosskey, R.W. (1989) Chapter 24. Simuliidae. In: Evenhuis N.L. (Ed.), *Catalog of the Diptera of the Australasian and Oceanian Region*. Special Publication 86. Bishop Museum Press and E.J. Brill, Honolulu, Leiden, pp. 221–225. Available from: <http://hbs.bishopmuseum.org/aocat/pdf/24sim.pdf> (accessed 24 April 2019)
- Crosskey, R.W. (1990) *The natural history of blackflies*. John Wiley & Sons, Chichester, 711 pp.
- Crosskey, R.W. & Howard, T.M. (1997) *A New Taxonomic and Geographical Inventory of World Blackflies*. The Natural History Museum, London, 144 pp. Available from: <https://www.cabdirect.org/cabdirect/abstract/19970503020> (accessed 24 April 2019)
- Crosskey, R.W. & Howard, T.M. (2004) *A revised taxonomic and geographical inventory of world blackflies (Diptera: Simuliidae)*. The Natural History Museum, London, 178 pp. Available from: <http://blackflies.info/sites/blackflies.info/files/u13/Inventory.pdf> (accessed 24 April 2019)
- Cumming, J.M. & Wood, D.M. (2017) Adult morphology and terminology. Chapter 3. In: Kirk-Spriggs, A.H. & Sinclair, B.J. (Eds.), *Manual of Afrotropical Diptera. Volume 1. Introductory chapters and keys to Diptera families*. Suricata 4. South African Biodiversity Institute, Pretoria, pp. 89–133. Available from: <https://afrotropicalmanual.org> (accessed 24 April 2019)
- Currie, D.C. (1986) An annotated list of and keys to the immature black flies of Alberta. *Memoirs of the Entomological Society of Canada*, 134, 1–90.
<https://doi.org/10.4039/entm118134fv>

- Currie, D.C. & Adler, P.H. (2008) Global diversity of black flies (Diptera: Simuliidae) in freshwater. *Hydrobiologia*, 595, 469–475.
<https://doi.org/10.1007/s10750-007-9114-1>
- Currie, D.C. & Grimaldi, D. (2000) A new black fly (Diptera: Simuliidae) genus from mid Cretaceous (Turonian) amber of New Jersey. In: Grimaldi, D. (Ed.), *Studies on Fossils in Amber, with Particular Reference to the Cretaceous of New Jersey*. Backhuys Publishers, Leiden, pp. 473–485.
- Currie, D.C., Craig, D.A. & Moulton, J.K. (2018c) A new genus, *Protaustrosimulium*, for four species of Australian black flies (Diptera: Simuliidae). *Zootaxa*, 4521 (3), 301–334.
<https://doi.org/10.11646/zootaxa.4521.3.1>
- Daniels, G. (1978) A catalogue of the type specimens of Diptera in the Australian Museum. *Records of the Australian Museum*, 31, 411–471.
<https://doi.org/10.3853/j.0067-1975.31.1978.222>
- Davies, L. (1960) The first-instar larva of a species of *Prosimulium* (Diptera: Simuliidae). *The Canadian Entomologist*, 92, 81–84.
<https://doi.org/10.4039/Ent9281-2>
- Davies, D.M. & Györkös, H. (1988) Two new Australian species of Simuliidae (Diptera). *Journal of the Australian Entomological Society*, 27, 105–115.
<https://doi.org/10.1111/j.1440-6055.1988.tb01156.x>
- de Moor, F.C. (2017) Chapter 32. Simuliidae (Blackflies). In: Kirk-Sprigs, A.H. & Sinclair, B.J. (Eds.), *Manual of Afrotropical Diptera. Vol. 2. Nematocerous Diptera and lower Brachycera. Suricata 5*. South African National Biodiversity Institute, Pretoria, pp. 693–728. Available from: <https://afrotropicalmanual.org> (accessed 24 April 2019)
- Drummond, F.H.N. (1931) West Australian Simuliidae. *Journal and Proceedings of the Royal Society of Western Australia*, 18, 1–12.
<https://www.cabdirect.org/cabdirect/abstract/19351000159>
- Dumbleton, L.J. (1973) The genus *Austrosimulium* Tonnoir (Diptera: Simuliidae) with particular reference to the New Zealand fauna. *New Zealand Journal of Science*, 15, 480–548. (December, 1972). Available from: <http://www.bugz.org.nz/> (accessed 24 April 2019)
- Edwards, F.W. (1931) Simuliidae. In: *Diptera of Patagonia and South Chile. Part II. Fascicle 4. Nematocera*. British Museum (Natural History), London, pp. 121–154.
- Enderlein, G. (1921) Das System der Kriebelmücken (Simuliidae). *Deutsche tierärztliche Wochenschrift*, 29, 197–200.
- Enderlein, G. (1930) Der heutige Stand der Klassifikation der Simuliiden. *Archiv für Klassifikatorische und Phylogenetische Entomologie*, 1, 77–97.
- Exon, N., Kennett, J., Malone, M., Brinkhuis, H., Chaproniere, G., Ennyu, A., Fothergill, P., Fuller, M., Grauer, M., Hill, P., Janecek, T., Kelly, C., Latimer, J., McGonigal, K., Nees, S., Ninnemann, U., Nuernberg, D., Pekar, S., Pellaton, C., Pfuhl, H., Robert, C., Röhl, U., Schellenberg, S., Shevenell, A., Stickley, C., Suzuki, N., Touchard, Y., Wei, W. & White, T. (2002) Drilling reveals climatic consequences of Tasmanian Gateway opening. *Eos*, 83, 253–264.
<https://doi.org/10.1029/2002EO000176>
- Exon, N.F., Kennett J.P. & Malone, M.J. (2004) 1. Leg 189 synthesis: Cretaceous-Holocene history of the Tasmanian Gateway. In: Exon, N.F., Kennett, J.P., and Malone, M.J. (Eds.), *Proceedings of the Ocean Drilling Program, Scientific Results*, 189, 1–37.
<https://doi.org/10.2973/odp.proc.sr.189.101.2004>
- Figueiró, R., Calvet, A., Gil-Azevedo, L.H., Docile, T.N., Monteiro, R.F. & Maia-Herzog, M. (2015) Evidence of phenotypic plasticity of larvae of *Simulium subpallidum* Lutz in different streams from the Brazilian Cerrado. *Revista Brasileira de Entomologia*, 59, 28–31.
<https://doi.org/10.1016/j.rbe.2015.02.003>
- Gil-Azevedo, L.H. (2010) Análise Filogenética de Simuliidae (Insecta, Diptera, Culicomorpha), com Revisão de *Lutzsimulium* e das Espécies Australianas de *Paracnephia*. Ph. D. Thesis, Universidade Federal do Rio de Janeiro, Museu Nacional, Programa de Pós-Graduação em Zoologia, Rio de Janeiro, pp. 295.
- Gil-Azevedo, L.H. & Maia-Herzog, M. (2007) Preliminary considerations on phylogeny of Simuliidae genera from Southern Hemisphere (Insecta, Diptera). *Zootaxa*, 1643 (1), 39–68.
<https://doi.org/10.11646/zootaxa.1643.1.2>

- Hernández-Triana, L.M., Montes De Oca, F., Prosser, S.W.J., Hebert, P.D.N., Gregory, T.R. & McMurtrie, S. (2017) DNA bar-coding as an aid for species identification in austral black flies (Insecta: Diptera: Simuliidae). *Genome*, 60, 348–357.
<https://doi.org/10.1139/gen-2015-0168>
- Jell, P.A. & Duncan, P.M. (1986) Invertebrates, mainly insects, from the freshwater, Lower Cretaceous, Koonwarra Fossil Beds (Korumburra Group), South Gippsland, Victoria. *Memoirs of the Association of Australasian Paleontologists*, 3, 111–205.
- Jell, P.A. (2004) The fossil insects of Australia. *Memoirs of the Queensland Museum*, 50, 1–124. Available from: [http://www.qm.qld.gov.au/~media/Documents/QM/About Us/Publications/Memoirs - Nature/N50-1-2/50-1-jell.pdf](http://www.qm.qld.gov.au/~media/Documents/QM/About%20Us/Publications/Memoirs%20-%20Nature/N50-1-2/50-1-jell.pdf)
- Keast, A. (1981) Ecological biogeography of Australia. *Monographiae Biologicae*, 41, 1–2061.
- Lichtwardt, R.W. & Williams, M.C. (1990) Trichomycete gut fungi in Australian aquatic insect larvae. *Canadian Journal of Botany*, 68, 1057–1074.
<https://doi.org/10.1139/b90-133>
- MacGillivray, A.D. (1903) Winding elbow-pins. *Journal of the New York Entomological Society*, 11, 99–101. Available from: [https://www.jstor.org/stable/25003030?seq=1 - page_scan_tab_contents](https://www.jstor.org/stable/25003030?seq=1%20-%20page_scan_tab_contents) (accessed 24 April 2019)
- Mackerras, M.J. & Mackerras, I.M. (1948) Simuliidae (Diptera) from Queensland. *Australian Journal of Scientific Research, Series B, Biological Sciences*, 1, 231–270.
<https://doi.org/10.1071/B19480231>
- Mackerras, I.M. & Mackerras, M.J. (1949) Revisional notes on Australasian Simuliidae (Diptera). *Proceedings of the Linnean Society of New South Wales*, 73, 372–405.
Available from: <http://www.biodiversitylibrary.org/page/35069387#page/454/mode/1up> (accessed 24 April 2019)
- Mackerras, M.J. & Mackerras, I.M. (1950) Notes on Australasian Simuliidae (Diptera). II. *Proceedings of the Linnean Society of New South Wales*, 75, 167–187.
Available from: <https://www.biodiversitylibrary.org/item/109152#page/209/mode/1up> (accessed 24 April 2019)
- Mackerras, I.M. & Mackerras, M.J. (1952) Notes on Australasian Simuliidae (Diptera). III. *Proceedings of the Linnean Society of New South Wales*, 77, 104–113. Available from: <https://www.biodiversitylibrary.org/item/108648#page/166/mode/1up> (accessed 24 April 2019)
- Mackerras, M.J. & Mackerras, I.M. (1955) Notes on Australasian Simuliidae (Diptera). IV. *Proceedings of the Linnean Society of New South Wales*, 80, 105–112. Available from: <https://www.biodiversitylibrary.org/item/108603#page/127/mode/1up> (accessed 24 April 2019)
- Martin, J., Guryev, V., Macdonald, S.M., Blinov, A. & Edward, D.H.D. (2003) Phylogenetic relationships of *Archaeochlus* Brundin, *Austrochilus* Cranston and *Afrochilus* Freeman (Diptera: Chironomidae), basal genera with a Gondwanan connection. *Cimbebasia*, 19, 141–151.
- McAlpine, J.F. (1981) Morphology and terminology—adults. In: McAlpine, J.F., Peterson, B.V., Shewell, G.E., Teskey, H.J., Vockeroth, J.R. & Wood, D.M. (Eds.), *Manual of Nearctic Diptera. Vol. 1. Monograph 27*. Research Branch, Agriculture Canada, Ottawa, pp. 9–63. Available from: http://publications.gc.ca/collections/collection_2016/aac-aafc/A54-3-27-eng.pdf (accessed 24 April 2019)
- McIver, S. (1987) Sensilla of haematophagous insects sensitive to vertebrate host-associated stimuli. *International Journal of Tropical Insect Sciences*, 8, 627–635.
<https://doi.org/10.1017/S1742758400022712>
- Moulton, J.K. (2000) Molecular sequence data resolves basal divergences within Simuliidae (Diptera). *Systematic Entomology*, 25, 95–113.
<https://doi.org/10.1046/j.1365-3113.2000.00097.x>
- Moulton, J.K. (2003) Can the current molecular arsenal adequately track rapid divergence events within Simuliidae (Diptera)? *Molecular Phylogenetics and Evolution*, 27, 45–57.
[https://doi.org/10.1016/S1055-7903\(02\)00397-4](https://doi.org/10.1016/S1055-7903(02)00397-4)
- Moulton, J.K., Adler, P.H. & Prince, J. (2004) An unusual new species of *Paracnephia* Rubtsov (Diptera: Simuliidae) from Western Australia. *Zootaxa*, 409 (1), 1–12.
<http://dx.doi.org/10.11646/zootaxa.409.1>
- Moulton, J.K., Currie, D.C. & Craig, D.A. (2018) A new genus, *Ectemnoides*, for seven species of Australian Gondwanan Simuliidae (Diptera), with description of a novel form of larval attachment. *Insect Systematics and Diversity*, 2 (4), 1–54.
<http://dx.doi.org/10.1093/isd/ixy009>
- Nowell, A.M.R. & Jumars, P.A. (1984) Flow environments of aquatic benthos. *Annual Reviews of Ecology and Systematics*, 15,

303–328.

<https://doi.org/10.1146/annurev.es.15.110184.001511>

Okazawa, T. & Nodasaka, Y. (1982) Morphological observations on the first- and last-instar larvae of the genus *Gigantodax* (Diptera: Simuliidae). *Medical Entomology and Zoology*, 33, 95–103.

<https://doi.org/10.7601/mez.33.95>

Palmer, R.W. & Craig, D.A. (2000) An ecological classification of primary labral fans of filter-feeding black fly (Diptera: Simuliidae). *Canadian Journal of Zoology*, 78, 199–218.

<https://doi.org/10.1139/z99-205>

Prince, J. (1980) *Resource partitioning in a guild of stream insects*. M.Sc. Thesis. University of Western Australia, Perth, 129 pp.

Rees, A.B.H. & Cwynar, L.C. (2010) A test of Tyler's Line—response of chironomids to a pH gradient in Tasmania and their potential as a proxy to infer past changes in pH. *Freshwater Biology*, 55, 2521–2540.

<https://doi.org/10.1111/j.1365-2427.2010.02482.x>

Rix, M.G. & Harvey, M.S. (2012) Phylogeny and historical biogeography of ancient assassin spiders (Araneae: Archaeidae) in the Australian mesic zone: Evidence for Miocene speciation within Tertiary refugia. *Molecular Phylogenetics and Evolution*, 62, 375–396.

<https://doi.org/10.1016/j.ympev.2011.10.009>

Rix, M.G., Edwards, D.L., Byrne, M. & Harvey, M.S. (2015) Biogeography and speciation of terrestrial fauna in the south–western Australian biodiversity hotspot. *Biological Reviews*, 90, 762–793.

<https://doi.org/10.1111/brv.12132>

Rosenbaum, G. (2018) The Tasmanides: Phanerozoic tectonic evolution of eastern Australia. *Annual Review of Earth and Planetary Sciences*, 46, 291–325.

<https://doi.org/10.1146/annurev-earth-082517-010146>

Ross, D.H. & Craig, D.A. (1978) The seven larval instars of *Prosimulium mixtum* Syme and Davies and *P. fuscum* Syme and Davies (Diptera: Simuliidae). *Canadian Journal of Zoology*, 57, 290–300.

<https://doi.org/10.1139/z79-032>

Rothfels, K.H. (1979) Cytotaxonomy of Black Flies. *Annual Reviews of Entomology*, 24, 507–539.

<https://doi.org/10.1146/annurev.en.24.010179.002451>

Rubtsov, I.A. (1940) *Blackflies (Fam. Simuliidae). Fauna USSR. No. 23. Insects, Diptera 6 (6)*. Akademii Nauk SSSR, Moscow & Leningrad, ix +532 pp. [in Russian with English summary]

Sasaki, H., Nishijima, Y. & Ono, H. (1985) Studies on the relation between blood sources and the shape of the fore tarsal claw of the female black flies in Hokkaido (Diptera: Simuliidae). *Journal of the College of Dairying*, 11, 187–192.

Shewell, G.E., (1955) Identity of the black fly that attacks ducklings and goslings in Canada (Diptera: Simuliidae). *Canadian Entomologist*, 87, 345–349.

<https://doi.org/10.4039/Ent87345-8>

Shiel, R.J., Koste, W. & Tan, I.W. (1989) Tasmania revisited: rotifer communities and habitat heterogeneity. *Hydrobiologia*, 186/187, 239–245.

<https://doi.org/10.1007/BF00048919>

Smart, J. (1945) The classification of the Simuliidae (Diptera). *Transaction of the Royal Entomological Society of London*, 95, 463–532.

<https://doi.org/10.1111/j.1365-2311.1945.tb00437.x>

Sniderman, J.M.K., Woodhead, J.D., Hellstrom, J., Jordan, G.J., Russell, N., Drysdale, R.N., Tyler J.J. & Porch, N. (2016) Pliocene reversal of late Neogene aridification. *Proceeding of the National Academy of Science*, 113, 1999–2004.

<https://doi.org/10.1073/pnas.1520188113>

Strickland, E.H. (1913) Further observations on the parasites of *Simulium* larvae. *Journal of Morphology*, 24, 43–94.

<https://doi.org/10.1002/jmor.1050240103>

Sutcliffe, J.F., Shipp, J.L. & Kokko, E.G. (1987) Ultrastructure of the palpal bulb sensilla of the black fly *Simulium arcticum* (Diptera: Simuliidae). *Journal of Medical Entomology*, 24, 324–331.

<https://doi.org/10.1093/jmedent/24.3.324>

Takaoka, H. & Adler, P.H. (1997) A new subgenus, *Simulium* (*Daviesellum*), and a new species, *S. (D.) courtneyi*, (Diptera:

- Simuliidae) from Thailand and Peninsular Malaysia. *Japanese Journal of Tropical Medicine and Hygiene*, 25, 17–27.
<https://doi.org/10.2149/tmh1973.25.17>
- Taylor, G.S., Braby, M.F., Moir, M.L., Harvey, M.S., Sands, D.P.A., New, T.R., Kitching, R.L., McQuillan, P.B., Hogendoorn, K., Glatz, R.V., Andren, M., Cook, J.M., Henry, S.C., Valenzuela, I. & Weinstein, P. (2018) Strategic national approach for improving the conservation management of insects and allied invertebrates in Australia. *Austral Entomology*, 57, 124–149.
<https://doi.org/10.1111/aen.12343>
- Thompson, D.L. & Stillwell, J.D. (2010) Early Aptian (Early Cretaceous) freshwater bivalves from the Australian–Antarctic rift, southeast Victoria. *Alcheringa*, 34, 345–357.
<https://doi.org/10.1080/03115511003789023>
- Tonnoir, A.L. (1925) Australasian Simuliidae. *Bulletin of Entomological Research*, 15, 213–255.
<https://doi.org/10.1017/S0007485300046198>
- Toussaint, E.F.A., Hendrich, L., Escalona, H.E., Porch, N. & Balke, M. (2016) Evolutionary history of a secondary terrestrial Australian diving beetle (Coleoptera, Dytiscidae) reveals a lineage of high morphological and ecological plasticity. *Systematic Entomology*, 41, 650–657.
<https://doi.org/10.1111/syen.12182>
- Trayler, K.M., Davies, J.A., Horowitz, P. & Morgan, D. (1996) Aquatic fauna of the Warren bioregion, south-west Western Australia: does reservation guarantee preservation? *Journal of the Royal Society of Western Australia*, 79, 281–291. Available from: <http://researchrepository.murdoch.edu.au/5783/> (accessed 17 April 2019)
- Unmack, P.J. (2001) Biogeography of Australian freshwater fishes. *Journal of Biogeography*, 28, 1053–1089.
<https://doi.org/10.1046/j.1365-2699.2001.00615.x>
- Unmack, P.J. (2013) 2—Biogeography. In: Humphries, P. & Walker, K. (Eds.), *Ecology of Australian freshwater fishes*. CSIRO Publishing, Collingwood, pp. 25–48.
- Unmack, P.J., Hammer, M.P., Adams, M., Johnson, J.B. & Dowling, T.E. (2013) The role of continental shelf width in determining freshwater phylogeographic patterns in south-eastern Australian pygmy perches (Teleostei: Percichthyidae). *Molecular Ecology*, 22, 1683–1699.
<https://doi.org/10.1111/mec.12204>
- Van Oye, P. (1936) Observations sur la biologie des larves de *Simulium* (*Melusina*) Diptère. *Memoires Musee Royal d'histoire Naturelle Belgique*, Series II, Fasc. 3, 445–455.
- Webb, J.A. & James, J.M. (2006) Karst evolution of the Nullarbor Plain, Australia. In: Harmon, R.S. & Wicks, C. (Eds.), Perspectives on karst geomorphology, hydrology, and geochemistry—A tribute volume to Derek C. Ford and William B. White: *Geological Society of America Special Paper*, 404, pp. 65–78.
[https://doi.org/10.1130/2006.2404\(07\)](https://doi.org/10.1130/2006.2404(07))
- White, L.T., Gibson, G.M. & Lister, G.S. (2013) A reassessment of paleogeographic reconstructions of eastern Gondwana: bringing geology back into the equation. *Gondwana Research*, 24, 984–998.
<https://doi.org/10.1016/j.gr.2013.06.009>
- Williams, W.D. (1980) *Australian freshwater life: the invertebrates of Australian inland waters*. 2nd Edition. The Macmillan Company of Australia Pty., Ltd., Melbourne, 321 pp.
- Williams, W.D. (1981) 38. Inland aquatic systems: an overview. In: Keast, A. (Ed.), *Ecological biogeography of Australia*. W. Junk, The Hague, pp. 1081–1099.
- Wood, D.M. & Borkent, A. (1982) Description of the female of *Parasimulium crosskeyi* Peterson (Diptera: Simuliidae) and a discussion of the phylogenetic position of the genus. *Memoirs of the Entomological Society of Washington*, 10, 193–210.
- Woodhead, J., Hand, S.J., Archer, M., Graham, I., Sniderman, K., Arena, D.A., Black, K.H., Godthelp, H., Creaser, P. & Price, E. (2016) Developing a radiometrically-dated chronologic sequence for Neogene biotic change in Australia, from the Riversleigh World Heritage Area of Queensland. *Gondwana Research*, 29, 153–167. <https://doi.org/10.1016/j.gr.2014.10.004>
- Wygodzensky, P. & Coscarón S. (1962) On the relationship and zoogeographic significance of *Austrosimulium anthracinum* (Bigot), a blackfly from southern South America (Diptera: Simuliidae). *Pacific Insects*, 4, 235–244.
[http://hbs.bishopmuseum.org/pi/pdf/4\(1\)-235.pdf](http://hbs.bishopmuseum.org/pi/pdf/4(1)-235.pdf)

Australian Flies. *In*: Pape, T., Bickel, D. & Meier, R. (Eds.), *Diptera Diversity: Status, Challenges and Tools*. Koninklijke Brill NV, Leiden, pp. 227–256.

<https://doi.org/10.1163/ej.9789004148970.1-459.39>

Zwick, P. (1981a) 41. Plecoptera. *In*: Keast, A. (Ed.), *Ecological biogeography of Australia*. W. Junk, The Hague, pp. 1171–1182.

Zwick, P. (1981b) 42. Blephariceridae. *In*: Keast, A. (Ed.), *Ecological biogeography of Australia*. W. Junk, The Hague, pp. 1185–1193.